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RESEARCH

A Bioenergetics Approach to Setting Conservation Objectives for Non-Breeding Shorebirds in California's Central Valley

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ABSTRACT

An extensive network of managed wetlands and flooded agriculture provides habitat for migrating and wintering shorebirds in California's Central Valley. Yet with over 90% of historical wetlands in the region lost, Central Valley shorebird populations are likely diminished and limited by available habitat. To identify the timing and magnitude of any habitat limitations during the non-breeding season, we developed a bioenergetics model that examined whether currently available shorebird foraging habitat is sufficient to meet the daily energy requirements of the shorebird community, at either the baseline population size surveyed from 1992 to 1995 or double this size, which we defined as our long-term (100-year) population objectives. Using recent estimates of the extent of managed wetlands and flooded agriculture, satellite imagery of surface water, energy content of benthic invertebrates, and shorebird metabolic rates, we estimated that shorebird foraging habitat in the Central Valley is currently limited during the fall. If the population sizes were doubled, we estimated substantial energy shortfalls in the fall (late July–September) and spring (mid-March–April) totaling 4.02 billion kJ (95% CI: 2.23–5.83) and 7.79 billion kJ (2.00–14.14), respectively. We then estimated long-term habitat objectives as the minimum additional shorebird foraging habitat required to eliminate these energy shortfalls; the corresponding short-term (10-year) habitat objectives are to maintain an additional 2,160 ha (5,337 ac) of shallow (<10 cm) open water area in the fall and 4,692 ha (11,594 ac) in the spring. Because the Central Valley is one of the most important regions in the Pacific Flyway for migrating and wintering shorebirds, we expect that achieving these habitat objectives will benefit shorebirds well beyond the Central Valley. Our bioenergetics approach provides a transparent, repeatable process for identifying the timing and magnitude of habitat limitations as well as the most efficient strategies for achieving conservation objectives.

KEY WORDS

Benthic invertebrates, California, Central Valley Joint Venture, flooded agriculture, habitat objectives, managed wetlands, shorebirds

INTRODUCTION

The Central Valley of California is one of the most important regions for migrating and wintering shorebirds (Order: Charadriiformes; Sub-Orders: Scolopaci, Charadrii) in western North America with at least half a million birds using the region each year (Shuford et al. 1998). Yet, 90% of the Central Valley's historical wetlands have been lost, primarily as a result of water diversion, the construction of dams and levees for flood control, and conversion to intensive agriculture (Frayer et al. 1989). Thus, Central Valley shorebird populations were likely once much larger, and now may be limited by the availability of suitable foraging habitat (Page and Gill 1994; Shuford et al. 1998). Because the quality and quantity of non-breeding habitat can have important effects on avian body condition, survival, migration timing, and reproductive success (Raveling and Heitmeyer 1989; Sherry and Holmes 1996; Saino et al. 2004; Burton et al. 2006), the quality and quantity of Central Valley wetlands during the non-breeding season can significantly affect shorebird population dynamics and shorebird conservation well beyond the Central Valley.

There is strong interest in restoring and managing Central Valley wetlands and flooded agricultural lands to provide important ecosystem services and recreational opportunities for people, in addition to essential habitat for wildlife communities (Zedler and Kercher 2005). An extensive network of restored and managed wetlands and post-harvest flooded rice, corn, and other crops currently provide substantial habitat for non-breeding shorebirds in the Central Valley (Fleskes et al. 2012; Strum et al. 2013; Reiter et al. 2015b). However, the timing, extent, and depth of flooding can greatly affect their value as shorebird foraging habitat (CVJV 2006). As the availability and cost of water in the Central Valley varies with changing supply and demand, drought conditions, and the effects of climate change (Hanak and Lund 2012), the ability to supply water where and when it is most needed will maximize the benefits of this limited resource to non-breeding shorebirds.

The Central Valley Joint Venture (CVJV; *http://www.centralvalleyjointventure.org/*), established in 1988, is a coalition of 20 state, federal, and private partners with the common goal of providing sufficient habitat for migrating and resident birds in the Central Valley of California. In their most recent implementation plan, the CVJV developed population objectives for non-breeding shorebirds in the Central Valley for the first time, and adopted a bioenergetics modeling approach to evaluate the capacity of Central Valley managed wetlands and flooded agriculture to meet the energy requirements of shorebirds throughout the non-breeding season (CVJV 2006). This approach can be used to identify shortfalls in energy supply, and estimate the extent and timing of additional habitat necessary to meet the energy needs at specified population levels, but a paucity of necessary data limited the application of the bioenergetics model in the 2006 implementation plan. Yet it was apparent that non-breeding shorebirds use Central Valley wetlands over a much longer period of time (July–May) than non-breeding waterfowl (August–March; CVJV 2006). Flooding schedules for managed wetlands are primarily focused on meeting waterfowl needs (mid-September to mid-March), which also largely overlaps with the timing of post-harvest flooding in agriculture. Thus, foraging habitat for non-breeding shorebirds was thought to be limited in July–September and March–May. Habitat and food limitations during these periods are especially detrimental to shorebird populations, because they coincide with the timing of migration and molt.

Here, we describe our process for setting long-term (i.e., 100-year) population objectives for non-breeding shorebirds that depend on wetland habitats in the Central Valley and for estimating the total daily energy requirement of the shorebird community at these population levels. We developed new estimates of the quantity and quality of available shorebird foraging habitat throughout the non-breeding season, including the proportion of wetlands and post-harvest flooded crops that have open water, the proportion that are of suitable depth for foraging, and their energy content. We then developed a bioenergetics model (1) to evaluate whether currently available shorebird foraging habitat is sufficient to meet those daily energy requirements and (2) to identify the timing and magnitude of any energy shortfalls. Finally, we estimated long-term (100-year) habitat objectives as the additional foraging habitat required to eliminate these shortfalls, and identified

short-term (10-year) habitat objectives to track progress toward the long-term objectives.

MATERIALS AND METHODS

Study Area

The Central Valley of California extends more than 400 km north to south, and is bounded by the Sierra Nevada to the east and the Coast Ranges to the west (Figure 1). The valley is subdivided hydrologically into the Sacramento Valley to the north and the San Joaquin Valley to the south, each drained by a major river of the same name. The Sacramento–San Joaquin Delta, formed by the confluence of these two rivers, drains into the San Francisco Estuary to the west. The southernmost portion of the Central Valley is hydrologically distinct and separate from the rest of the San Joaquin Valley; in all but the wettest years, it is a terminal basin with rivers that once drained into Tulare Lake and several smaller lakes and sloughs now dammed in upstream reservoirs. The primary focus area of the CVJV is largely delineated by the Jepson boundary for the Great Central Valley region (Hickman 1993), and is subdivided into nine planning basins: Butte, Colusa, American, Sutter, Yolo, Suisun, Delta, San Joaquin, and Tulare. Our study addressed all but the Suisun basin, which is dominated by Suisun Marsh, a mosaic of brackish managed and tidally influenced wetlands with distinct habitat availability dynamics that are beyond the current scope of our bioenergetics modeling.

Long-Term (100-year) Population Objectives

Population objectives are often set for individual species (e.g., Dybala et al. 2017, this volume), but we assumed all shorebird species that depend on wetland habitats (i.e., managed wetlands and flooded agricultural fields) would depend on similar food resources during the non-breeding season, defined as 1 July through 15 May, such that they are directly competing for the same pool of calories. From a bioenergetics perspective, the carrying capacity of Central Valley wetlands depends on the size of the entire non-breeding shorebird community and cannot be readily assessed for each species independently. Consequently, we adopted the approach used in other energetics-based conservation plans (e.g., Loesch et al. 2000; IWJV 2013) and in previous efforts in setting population objectives for non-breeding shorebirds in the region (Hickey et al. 2003; CVJV 2006) by setting population objectives that represent the total number of shorebirds that the Central Valley will be able to support during each day of the non-breeding season.

The Central Valley is an important location on the Pacific Flyway for both non-breeding shorebirds and waterfowl, supporting up to half a million shorebirds (Shuford et al. 1998) and up to 60% of all waterfowl in the Pacific Flyway (CVJV 2006). For waterfowl, this proportion can be used to scale continental population objectives down to Central Valley population objectives (CVJV 2006; Petrie et al. 2011), but we could not take this approach for shorebirds because continental population objectives do not yet exist. However, we assumed that the Central Valley also supports a considerable proportion of shorebirds in the Pacific Flyway, particularly with Central Valley wetlands and flooded agriculture recognized as sites of international importance for shorebirds (WHSRN c2009). Further, although long-term trend data are lacking (Shuford et al. 1998), we assumed that the loss of over 90% of historical wetlands in the Central Valley (Frayer et al. 1989) has likely resulted in a decline in the size of the non-breeding shorebird community using the Central Valley by at least 50% from pre-1900 levels to the present. Therefore, we reasoned that the international importance of the Central Valley to shorebirds, and the declines from historical levels, warranted setting relatively large population objectives, and, in lieu of continental objectives scaled down to the Central Valley, we set long-term (100-year) population objectives that are based on doubling the size of the non-breeding shorebird community, a rough approximation of pre-1900 population levels. Although it may no longer be possible to restore wetlands to their pre-1900 extent, the amount of foraging habitat required to support a shorebird community of this size may be far less, depending on how wetlands and flooded agriculture are managed.

Comprehensive surveys of shorebirds in Central Valley managed wetlands and flooded agricultural fields were conducted between 1992 and 1995 (Shuford et al. 1998), and we used these data to represent our baseline population size. The baseline

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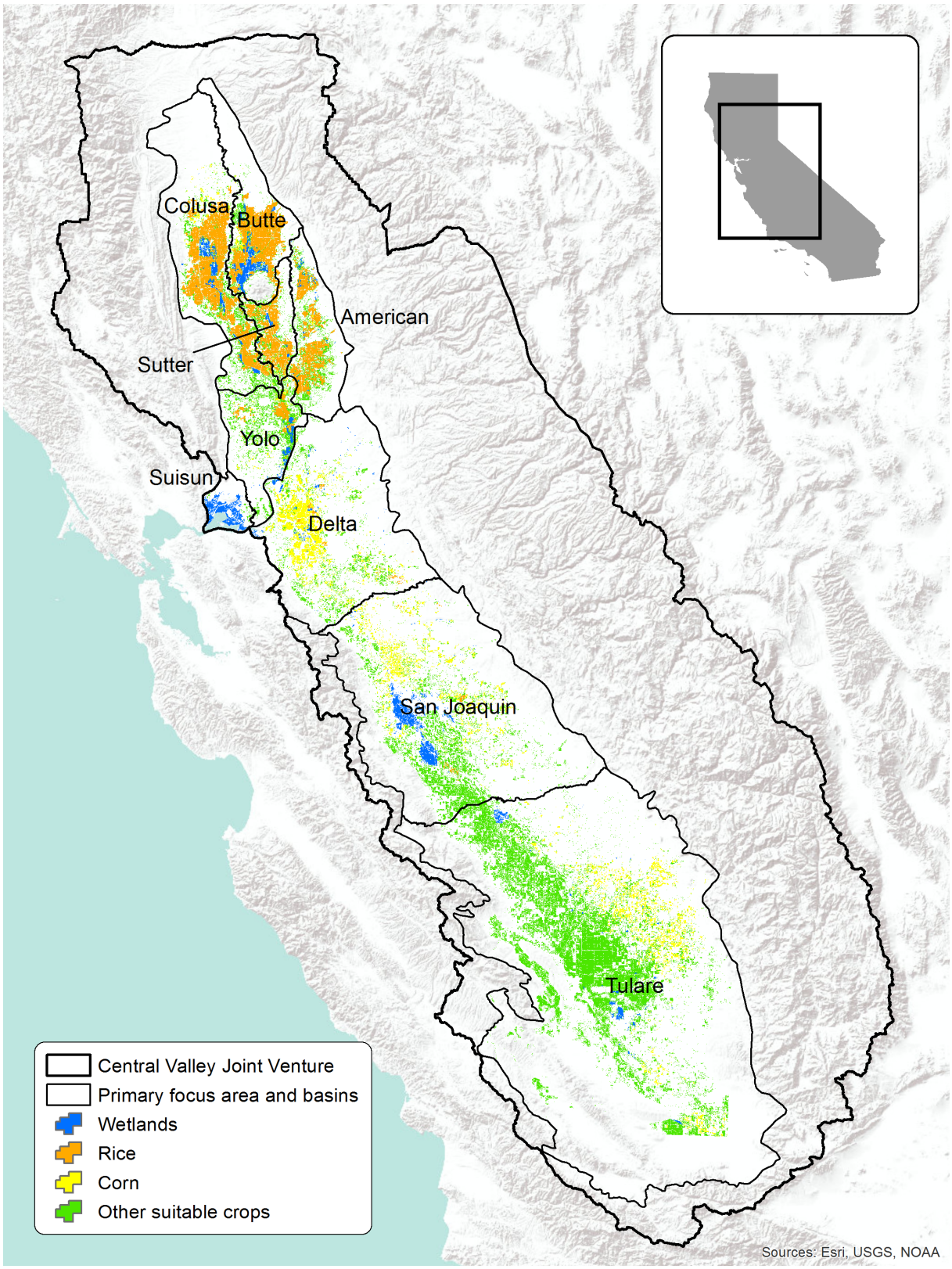

Figure 1 Central Valley Joint Venture boundary, primary focus area, and planning basins, shown with wetlands (2009) and the average distribution of three crop classes that are potentially suitable habitat for non-breeding shorebirds (2007–2014).

surveys were conducted during four periods within the non-breeding season (August, November, late January–early February, and April). Excluding rare or uncommon species, Shuford et al. (1998) recorded 19 shorebird species, of which 12 currently have national conservation status designations including: requires immediate conservation action (IM), needs management attention (MA), increased climate change vulnerability (CCV), and common shorebird in decline (D) (Table 1; U.S. Shorebird Conservation Plan Partnership 2015). We focused our population and habitat objectives solely on these shorebird species that depend on wetland habitats, and we assumed that wetland foraging habitat was the primary limiting factor. Although some of these species also use upland habitats, Shuford et al. (1998) did not adequately survey these areas, and we assumed the numbers recorded in managed wetlands and flooded agricultural fields reflected the degree to which these species rely on wetland habitats.

From the baseline survey data, we estimated the daily size of the shorebird community between August and April by fitting a generalized additive model with a Poisson error distribution to the total shorebird counts, including a smoother for day of year (where 1 July = Day 1; Wood 2006). We assigned August counts to Day 46 (15 August), November counts to Day 138 (15 November), late January–early February counts to Day 215 (31 January), and April counts to Day 289 (15 April). We excluded data from the January 1995 survey because there was record winter rainfall in California, with a much higher number of shorebirds present in the Central Valley that may have been displaced from deteriorating conditions on the California coast or attracted to rain-supplemented habitat in the Central Valley (Warnock et al. 1995; Shuford et al. 1998), and we wanted to set a baseline that reflects more typical habitat availability. We used the model to estimate the daily size of the baseline population between 15 August and 15 April, and we calculated the daily population objectives as double the baseline estimates. We extrapolated these population objectives to cover the rest of the non-breeding season (1 July–15 August and 15 April–15 May), by assuming start (1 July) and end (15 May) points of 50,000 shorebirds (CVJV 2006) and a linear rate of change between 1 July and 15 August

Table 1 Central Valley shorebird species observed during baseline non-breeding season surveys 1992–1995 (Shuford et al. 1998), shown with current conservation status and average body mass estimates. The <0.05% of shorebirds classified by Shuford et al. (1998) as "other" (uncommon or rare) species are not shown.

Species	Continental conservation status [b]	Average body mass (g) [c]
Black-Necked Stilt (*Himantopus mexicanus*)		170
American Avocet (*Recurvirostra americana*) [a]	CCV	305
Black-Bellied Plover (*Pluvialis squatarola*)	CCV	250
Snowy Plover (*Charadrius nivosus*)	IM	42
Semipalmated Plover (*Charadrius semipalmatus*)		47
Killdeer (*Charadrius vociferus*) [a]	D	97
Greater Yellowlegs (*Tringa melanoleuca*) [a]		153
Willet (*Tringa semipalmata*)	MA	271
Lesser Yellowlegs (*Tringa flavipes*)	MA	78
Whimbrel (*Numenius phaeopus*) [a]	IM	380
Long-Billed Curlew (*Numenius americanus*) [a]	MA	587
Marbled Godwit (*Limosa fedoa*)	MA	359
Dunlin (*Calidris alpina*) [a]	MA	47
Least Sandpiper (*Calidris minutilla*)		23
Western Sandpiper (*Calidris mauri*) [a]	CCV	28
Long-Billed Dowitcher (*Limnodromus scolopaceus*) [a]		105
Wilson's Snipe (*Gallinago delicata*) [a]		122
Wilson's Phalarope (*Phalaropus tricolor*)		60
Red-Necked Phalarope (*Phalaropus lobatus*)	D	37

a. Species for which the Central Valley population is of primary importance (i.e., populations are likely to be larger in the Central Valley than in other shorebird planning regions in the United States; Hickey et al. 2003)

b. Conservation status designations were drawn from the U.S. Shorebird Conservation Plan (USCPP 2015) and the highest designation of any sub-population are shown: requires immediate conservation action (IM), needs management attention (MA), increased climate change vulnerability but not IM or MA (CCV), and common shorebird in decline (D). The IM and MA designations also indicate that the species meets the criteria for U.S. Fish and Wildlife Service Birds of Conservation Concern.

c. Average body mass estimates were drawn from Dunning (2008); where separate estimates for average male and female body mass were provided, we used the mean.

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(increasing) and between 15 April and 15 May (decreasing).

Energy Needs

We estimated the daily energy requirement of the non-breeding shorebird community based on estimates of metabolic rate and energy assimilation efficiency. Metabolic rate generally increases with body mass, so, to estimate the metabolic rate of an average shorebird in the baseline population, we compiled body mass estimates for each species (Dunning 2008). Where separate estimates of male and female body masses were available, we took the mean value, equivalent to assuming a 1:1 sex ratio in the population. Using the baseline surveys, we then estimated the weighted average body mass of an individual shorebird during each survey, with weights for the body mass of each species determined by the proportion of the community comprising that species during each survey. Where Shuford et al. (1998) reported mixed-species groups (e.g., sandpipers and phalaropes), we apportioned these according to the ratios of the relevant species identified during the same survey. However, unidentified dowitchers and yellowlegs in the Central Valley during the non-breeding season are most likely to be long-billed dowitchers and greater yellowlegs (Shuford et al. 1998), so we assumed 100% belonged to these species. We excluded from estimates of weighted average body mass the <0.05% of shorebirds classified as "other" (uncommon or rare) species.

To estimate the temporal variation in weighted average body mass over the course of the non-breeding season resulting from changes in species composition, we fit a generalized additive model to the weighted average body mass estimate from each survey, including a smoother for day of year, where 1 July = Day 1. We used the model to estimate the daily average body mass of an individual shorebird between 15 August and 15 April. We extrapolated these body mass estimates to cover the entire non-breeding season (1 July–15 May) by assuming no change in the relative proportion of each species between 1 July and 15 August, or between 15 April and 15 May.

From these daily weighted average body mass estimates, we then estimated the daily average resting metabolic rate (RMR) and field metabolic rate (FMR) of an individual shorebird from allometric scaling equations developed for shorebirds (Kersten and Piersma 1987; Brand et al. 2013):

$$RMR_t = 437 \times m_t^{0.729} \quad (1)$$

$$FMR_t = 3 \times RMR_t \quad (2)$$

where m_t is body mass (kg) at time t and RMR_t and FMR_t are in kJ. *FMR* is higher than *RMR* because it takes into account additional energy expended for daily activities and thermoregulation (Kersten and Piersma 1987). Because not all energy consumed is assimilated, the actual daily energy intake requirement is higher than the *FMR*. Based on an assimilation efficiency estimate for shorebirds of 0.73 (Castro et al. 1989), we calculated daily energy intake (DEI_t in kJ) of each shorebird as:

$$DEI_t = FMR_t / 0.73 \quad (3)$$

Thus, we estimated the daily energy requirement (DER_t in kJ) of the entire non-breeding shorebird community as:

$$DER_t = DEI \times n_t \quad (4)$$

where n_t is the total number of individuals in the community at time t, for either the baseline population or the population objectives. We assumed that metabolic rate and thus *DER* increases substantially as birds prepare for spring migration by accumulating fat (Kersten and Piersma 1987; Warnock and Bishop 1998), and we increased the *DEI* and thus the *DER* from 1 March through 15 May by 33% (CVJV 2006).

Current Habitat Availability

To estimate the temporal variation in the average extent of foraging habitat available to shorebirds over the course of the non-breeding season, we estimated: (1) the total extent of potentially suitable land cover types, (2) the daily proportion of each land cover type that has open water throughout the non-breeding season, and (3) the daily proportion of the open water in each land cover type that is accessible to shorebirds (e.g., of a suitable depth).

Total Potential Habitat

We considered potentially suitable land cover types for non-breeding shorebirds to include managed wetlands and crops that are regularly flooded post-harvest and used by shorebirds, including rice, corn, other field crops, and row crops (Elphick 2000; Fleskes et al. 2012; Strum et al. 2013; Shuford et al. 2016). Although shorebirds in the Central Valley also use evaporation and sewage ponds (Shuford et al. 1998), we did not include these areas as potential habitat because they are known to expose shorebirds to extremely concentrated trace elements, salts, contaminants, and diseases (Ohlendorf 1993; CVJV 2006; Murray and Hamilton 2010; Davis and Hanson 2014), and some evaporation ponds are actively managed to discourage shorebird use (Davis and Hanson 2014). We also excluded alfalfa fields because we considered alfalfa generally too dense to be accessible to most shorebirds over the majority of the growing cycle, and they were not adequately surveyed by Shuford et al. (1998). We also excluded the considerable amount of corn grown in the San Joaquin and Tulare basins, which is rarely flooded post-harvest (Fleskes et al. 2013; Reiter et al. 2015a; Shuford et al. 2016).

For managed seasonal and semi-permanent wetlands, we used estimates reported from a GIS layer of Central Valley wetlands produced from 2009 satellite imagery (Petrik et al. 2014) supplemented by the estimated area of wetlands restored between 2009 and 2015 (2016 email from D. Fehringer, Ducks Unlimited, to K. Dybala, unreferenced, see "Notes"). For rice, corn, and other field and row crops, we compiled state-wide survey statistics from 2007 to 2014 (NASS c2016), which provided the best estimate of the annual total area planted in California. Our other field and row crops class included all those with state-wide totals reported (i.e., barley, beans, cotton, oats, safflower, sugarbeets, sunflower, wheat, and total vegetables). To estimate the extent of each crop class within each CVJV planning basin, we used a GIS layer that represented the consistent spatial distribution of each crop class between 2007 and 2014 in California (The Nature Conservancy, unpublished data, see "Notes"). We estimated the proportion of the pixels of each crop class that fell within each basin, and used these proportions to allocate the statewide totals among the basins. This approach allowed us to estimate the annual extent and 2007–2014 average extent of each crop class within the CVJV primary focus area and each planning basin.

Proportion Open Water

For each land cover type, we estimated the daily proportion that had open water using satellite imagery of surface water from Landsat 5 Thematic Mapper collected between January 2007 and June 2011 (*http://earthexplorer.usgs.gov*). The satellite imagery from multiple scenes covering the Central Valley were processed so that each 30m x 30m raster cell represented the probability of open water (<25% vegetation cover) in each half-month of each year (e.g., July 1–15, July 16–31; Reiter et al. 2015a). We combined the wetlands and crop class GIS layers used above (Petrik et al. 2014; The Nature Conservancy, unpublished data, see "Notes") to generate a single land cover raster, and overlaid it with each satellite image to estimate the proportion of cells within each land cover type that had open water and the proportion of cells sampled (i.e., not masked by clouds or shadows).

For each land cover type, we modeled the proportion of cells with open water as a function of day of year, where Day 1 = July 1. We fit a generalized additive mixed model with a binomial error distribution (Wood 2006; Wood and Scheipl 2014), including random intercepts for each non-breeding season (1 July–15 May), to account for non-independence of samples from the same season, and individual data point, to account for over-dispersion (Browne et al. 2005). We weighted each data point by the proportion of cells sampled in each half-month, and excluded data points with less than 50% of the land cover type sampled. We used the model to predict the daily proportion of each land cover type with open water between 1 July and 15 May.

Proportion Accessible

Wetlands and post-harvest flooded crops also vary in water depth, and many shorebird species do not forage in water >10 cm deep (Safran et al. 1997; Elphick and Oring 1998; Strum et al. 2013). For rice, we compiled depth data recently collected between

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mid-November and May, 2009–2013 (Strum et al. 2013; Sesser et al. 2014; Migratory Bird Conservation Partnership, unpublished data, see "Notes"). For all rice fields with an average water depth >0, we modeled the probability that the field was of suitable depth for shorebirds (<10 cm) as a function of day of year, where Day 1 = July 1. We again fit a generalized additive mixed model with a binomial error distribution, including random intercepts for individual fields and property IDs to account for repeated visits. We used the model to predict the daily proportion of the open water in rice that was accessible between 15 November and 15 May. We also assumed any open water in rice detected before 1 September would be on, average, not yet harvested, and thus not accessible to foraging shorebirds. Because we lacked data for the time-period between 1 September and 15 November, we initially assumed a symmetrical curve to predict daily proportion accessible during this period. However, based on expert opinion that fall flood-up happens at a faster rate than spring draw-down in rice (2015 in-person conversation among the Central Valley Joint Venture shorebird–waterbird working group, unreferenced, see "Notes"), we doubled the slope of the curve beginning 1 September. Between 1 April and 15 May, when rice fields are again flooded for planting, data were relatively limited, and we assumed the proportion accessible during this late spring flood-up would be similar to the fall flood-up.

We are unaware of comparable depth data collected throughout the non-breeding season for Central Valley wetlands or for corn and other post-harvest flooded crops. For wetlands, we developed estimates of the proportion of seasonal and permanent or semi-permanent wetlands that are of suitable shorebird depth throughout the year based on expert opinion (2015 email from C. Isola, U.S. Fish and Wildlife Service, to K. Dybala, unreferenced, see "Notes"). We also generated estimates of the confidence intervals around these estimates from a logistic distribution with a scale of 0.25. For corn and other crops, we assumed the proportion accessible would be similar to the proportion accessible in rice at the peak of flooding, and we assumed no temporal variation in the proportion accessible. We again assumed any open water detected in corn or other crops before 1 September would be before harvest. and not accessible to foraging shorebirds.

We calculated the total area of open water (TW) and accessible open water (TA) in each land cover type i at each daily time-step t as:

$$TW_{i,t} = T_i * PF_{i,t} \quad (5)$$

$$TA_{i,t} = TW_{i,t} * PA_{i,t} \quad (6)$$

where T_i is the total area of each land cover type, $PF_{i,t}$ is the proportion of each land cover type with open water (i.e., flooded), and $PA_{i,t}$ is the proportion of the open water area that is accessible to shorebirds (i.e., <10 cm). We also calculated the daily change in area of open water for each land cover type. We assumed that once water is applied to wetlands and post-harvest flooded crops, these areas generally remain flooded until draw-downs begin in the spring, so that an increase in the proportion open water between time-steps reflects the total area of newly added open water each day. For example, a change from 10% to 12% in the proportion open water ($PF_{i,t}$) reflects the addition of 2%, rather than a possible loss of 10% and the addition of a new 12% elsewhere. We estimated the area of newly added open water (WA) in each land cover type i at each daily time-step t as:

$$WA_{i,t} = \begin{cases} T_i * \left(PF_{i,t} - PF_{i,t-1}\right) & if\ PF_{i,t} > PF_{i,t-1} \\ 0 & otherwise \end{cases} \quad (7)$$

Similarly, we estimated the area of open water that will be lost before the next time-step ($WL_{i,t}$) as:

$$WL_{i,t} = \begin{cases} T_i * \left(PF_{i,t} - PF_{i,t+1}\right) & if\ PF_{i,t} > PF_{i,t+1} \\ 0 & otherwise \end{cases} \quad (8)$$

Current Energy Density

To estimate the energy available to shorebirds in newly flooded wetlands and agricultural fields, we compiled data from studies of benthic invertebrates in Central Valley managed wetlands or flooded rice fields during the non-breeding season (reviewed in Strum 2011). We included studies that reported taxon-specific benthic invertebrate density (individuals ha^{-1}) or taxon-specific biomass density (kg ha^{-1}) or both, including three studies in Central

Valley managed wetlands (Severson 1987; Sefchick 1992; Colwell et al. 1995) and two in flooded rice fields (Elphick 2000; Sesser et al. 2014; Point Blue Conservation Science and U.S. Geological Survey, unpublished data, see "Notes"). We excluded studies that reported results for only a subset of taxa. For each taxon reported in these five studies, we confirmed evidence of their presence in shorebird diets (Brooks 1967; Davis and Smith 1998; Sánchez et al. 2005; Andrei et al. 2007; Smith et al. 2012).

Estimates of taxon-specific biomass density (kg ha^{-1}) were not available for some of the samples in rice, so we converted the estimates of taxon-specific invertebrate density (individuals ha^{-1}) to estimates of biomass density using estimates of mean individual biomass (mg $individual^{-1}$). Estimates of mean individual biomass were derived from the three wetlands studies, supplemented by direct estimates of individual biomass from two additional studies (Sikora et al. 1977; Brand et al. 2013; Appendix A). Similarly, we converted the biomass density estimates in both rice and wetlands to estimates of taxon-specific energy density (MJ ha^{-1}) using taxon-specific estimates of energy content (MJ kg^{-1}) derived from published data (Cummins and Wuycheck 1971; Sikora et al. 1977; Driver 1981; Anderson and Smith 1998; Brand et al. 2013). We then summed the taxon-specific biomass density and energy density to estimate the total biomass density and energy density of all benthic invertebrates in each sample (see Appendix A for additional details). At each step, we propagated the uncertainty in the estimates of individual biomass, biomass density, and energy content to derive estimates of the standard error of the total biomass density and energy density in each sample (Ku 1966).

The depth of the benthic cores used in these studies ranged from 4 to 15 cm, but Elphick (2000) found no significant difference in invertebrate density between the top and bottom halves of an 8-cm core. We assumed biomass and energy density would also be fairly evenly distributed down to 8 cm, and, to be able to compare the results of these five studies, we adjusted the total biomass density and energy density estimates proportionally to a depth of 8 cm. We also assumed that because benthic invertebrates move vertically through the substrate (Charbonneau and Hare 1998), those up to 8 cm deep at the time of sampling will eventually become accessible to most shorebirds. Severson (1987) used cores varying between 6 cm and 10 cm in depth (2015 email from D. Severson, U.S. Fish and Wildlife Service, to K. Dybala, unreferenced, see "Notes"), but the original data were no longer available, and these estimates were not adjusted for depth.

To estimate the overall average energy density of benthic invertebrates in wetlands and rice, we fit two linear mixed-effects models (Bolker 2009; Bates et al. 2015) with log-transformed energy density as the response variable, and either a fixed effect of land cover type (wetlands or rice) or an intercept only. Both models included random intercepts for plot ID and study ID, and to give more weight to energy density estimates with smaller standard deviations, we weighted estimates by the inverse coefficient of variation (mean divided by standard deviation). We used the Akaike weights of each model to calculate the model-averaged predicted energy density for Central Valley managed wetlands and flooded rice with 95% confidence intervals (Burnham and Anderson 2002). We repeated this process to estimate the overall average biomass density of benthic invertebrates in wetlands and rice, for comparison with the estimate of 20 kg ha^{-1} in shorebird habitat in the Mississippi Alluvial Valley that had been previously adopted by the CVJV (2006).

We are unaware of any comparable data on the benthic invertebrates in other flooded crops, and we assumed that the energy density available in rice was representative of the energy density in all post-harvest flooded agricultural fields. In addition, we did not have sufficient data to examine regional differences or temporal variation in energy density, and we lacked data on benthic invertebrate growth rates throughout the non-breeding season. Invertebrate growth rates may vary widely among species, with temperature, and depending on management (Loughman and Batzer 1992; Duffy and LaBar 1994; Moss et al. 2009; Tapp and Webb 2015). Because of these uncertainties, we made the simplifying assumptions that there were no regional variations in energy density, and, to remain conservative in our estimates of energy supply, we assumed that any invertebrate growth over the non-breeding season was negligible.

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Bioenergetics Model

We developed a bioenergetics model, inspired by the TRUEMET model used in previous CVJV planning (CVJV 2006; Petrie et al. 2016) and other modeling efforts (Brand et al. 2013), that compares the daily energy needs of the shorebird community against the daily energy available across all land cover types, accounting for both dynamic habitat availability and consumption of food resources in previous time-steps. See Table 2 for a summary of all parameters used in the bioenergetics model.

At the start of each daily time-step, we estimated the energy supply (*ES*) and average energy density (*ED*) provided by each land cover type i at time t as:

$$ES_{i,t} = ER_{i,t-1} + WA_{i,t} * ED_{i,0} \quad (9)$$

$$ED_{i,t} = ES_{i,t} / TW_{i,t} \quad (10)$$

where $ER_{i,t-1}$ is the energy remaining in land cover type i at the end of the previous time-step (if any, described further below) and $ED_{i,0}$ is the average initial energy density (kJ ha^{-1}) of benthic invertebrates in each land cover type. We assumed that $ED_{i,0}$ is immediately available in newly added open water area, such that $ED_{i,t}$ is initially equal to $ED_{i,0}$. However, because some of this energy may be in deep water and inaccessible to shorebirds, we also estimated the energy accessible (EA) in each land cover type i at time t as:

$$EA_{i,t} = ES_{i,t} * PA_{i,t} \quad (11)$$

We assumed that shorebirds would draw their daily energy requirement (DER_t) from each land cover type in proportion to the energy accessible in each land cover type ($EA_{i,t}$). This is equivalent to assuming an ideal free distribution (Fretwell and Lucas 1969). However, if the DER_t was greater than the total energy accessible in all land cover types (TEA_t), we assumed all of the energy accessible ($EA_{i,t}$) was consumed. Thus, we estimated energy consumed (*EC*) in land cover type i at time t as:

$$EC_{i,t} = \begin{cases} DER_t * \left(EA_{i,t} / TEA_t\right) & if\ DER_t < TEA_t \\ EA_{i,t} & otherwise \end{cases} \quad (12)$$

where TEA_t is the sum total of $EA_{i,t}$ across all land cover types. We also estimated the daily shortfall in energy (S_t), if any, as:

$$S_t = \begin{cases} DER_t - TEA_t & if\ DER_t > TEA_t \\ 0 & otherwise \end{cases} \quad (13)$$

After consumption of accessible energy, we calculated the energy density remaining (*EDR*) in accessible open water of each land cover type i as:

$$EDR_{i,t} = \left(EA_{i,t} - EC_{i,t}\right) / TA_{i,t} \quad (14)$$

In addition to consumption, the energy supply ($ES_{i,t}$) may be reduced by losses in the area of open water in each land cover type before the start of the next time-step. However, we assumed that these losses would first be in the shallow areas accessible to shorebirds, in which the energy supply has already been at least partially consumed. Thus, we calculated the additional energy lost from a reduction in open water area ($EL_{i,t}$) as:

$$EL_{i,t} = \begin{cases} EDR_{i,t} * WL_{i,t} & if\ WL_{i,t} < TA_{i,t} \\ EDR_{i,t} * TA_{i,t} + ED_{i,t} * \left(WL_{i,t} - TA_{i,t}\right) & otherwise \end{cases} \quad (15)$$

where if the losses in open water habitat ($WL_{i,t}$) exceed the total area accessible ($TA_{i,t}$), all energy remaining in accessible areas is lost, in addition to some energy from the inaccessible areas.

Finally, we calculated the energy remaining (*ER*) in land cover type i at the end of time-step t as:

$$ER_{i,t} = ES_{i,t} - EC_{i,t} - EL_{i,t} \quad (16)$$

The $ER_{i,t}$ then carries forward, contributing to the energy supply ($ES_{i,t}$) at the start of the next time-step and is included in Equation 9 as $ER_{i,t-1}$. We implemented this set of equations in R, calculating each parameter iteratively for each daily time-step (R Core Team 2015); we have made the code available as the R package "bioenergmod" (Dybala 2016).

We used this bioenergetics model to evaluate whether the currently available shorebird foraging habitat is sufficient to meet the daily energy requirements (DER_t) of the non-breeding wetland-dependent shorebird community in the Central Valley. We ran this model with the daily energy requirements

Table 2 Summary of parameters used in the bioenergetics model for shorebirds in the Central Valley of California

Parameter	Description	Units
(A) Data inputs		
$ED_{i,0}$	Average energy density of benthic invertebrates in each land cover type i	kJ ha^{-1}
m_t	Weighted average body mass of an individual shorebird at a time t	kg
n_t	Size of the shorebird community at a time t, either baseline or population objectives	n
$PA_{i,t}$	Proportion of each land cover type with open water that is accessible to shorebirds at time t	-
$PF_{i,t}$	Proportion of each land cover type with open water at time t	-
T_i	Total area of each land cover type	ha
(B) Derived from inputs		
DER_t	Daily energy requirement of the shorebird community, derived from m and n using allometric scaling equations	kJ
$TA_{i,t}$	Total accessible open water area in each land cover type at time t, derived from T_i, $PF_{i,t}$, and $PA_{i,t}$	ha
$TW_{i,t}$	Total open water area in each land cover type at time t, derived from T_i and $PF_{i,t}$	ha
$WA_{i,t}$	Area of open water newly added at time t	ha
$WL_{i,t}$	Area of open water lost before time $t+1$	ha
(C) Model outputs		
$EA_{i,t}$	Energy accessible to shorebirds in each land cover type at time t	kJ
$EC_{i,t}$	Energy consumed in each land cover type at time t	kJ
$ED_{i,t}$	Average energy density of benthic invertebrates in each land cover type at time t, accounting for consumption	kJ ha^{-1}
$EDR_{i,t}$	Energy density remaining in accessible open water areas of each land cover type after consumption at time t	kJ ha^{-1}
$EL_{i,t}$	Energy lost at the end of time t from any losses in open water area before time $t+1$	kJ
$ER_{i,t}$	Energy remaining in each land cover type at the end of time step t that carries forward to the next time step	kJ
$ES_{i,t}$	Energy supply available in each land cover type i at time t	kJ
S_t	Shortfall in accessible energy needed to meet the daily energy requirement of the shorebird community at time t	kJ
TEA_t	Total energy accessible in all land cover types at time t	kJ

for both the baseline population size estimated between 1992 and 1995 (Shuford et al. 1998) and the population objectives defined above. We also ran the bioenergetics model including only the wetlands area to evaluate whether current wetland habitat availability and management practices are sufficient to meet the CVJV's goal that at least 50% of the shorebird energy needs should be met by wetlands from October through March, and 100% from July through September and April through May (CVJV 2006). Achieving this goal would limit reliance on flooded agricultural fields, the availability of which may change rapidly with changing economic and climatic conditions or environmental policies (Johnston and Carter 2000; Hagy et al. 2014; Hatfield et al. 2014).

We used Monte Carlo simulation to examine the uncertainty in our estimates of total energy accessible (TEA_t) and energy shortfall (S_t) resulting from the uncertainty in our estimates of energy density, the proportion open water, and the proportion accessible in each land cover type. For each of 10,000 iterations of the bioenergetics model, we generated random values of energy density drawn from a log-normal distribution with mean and standard deviation for each land cover type; we assumed corn and other crops had the same mean and standard deviation as rice. Similarly, we generated random values for the model parameters that predicted the daily proportion open water in each land cover type and the daily proportion accessible in rice. For the proportion accessible in seasonal and semi-permanent or permanent wetlands, we added error to the estimates derived from expert opinion drawn from a logistic distribution with a location of 0 and a scale of 0.25. For the proportion accessible in corn and other crops, for which no data were available, we generated estimates from a logistic distribution with location

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location and scale derived from the predicted value for rice during the peak of flooding, and we assumed no temporal variation.

Using 10,000 samples of each parameter as inputs into the bioenergetics model, we estimated the median of the TEA_t and S_t resulting from each iteration of the model, and the 95% confidence interval from the 2.5 and 97.5 percentiles. We considered any median $S_t > 0$ to indicate that currently available shorebird foraging habitat is not sufficient, on average, to meet the daily energy requirements. We also examined the sensitivity of the bioenergetics model to the uncertainty in each parameter by fitting the model with the lower or upper confidence limits of each parameter while holding all other parameters at their mean values and calculating the range of the cumulative total S_t over the course of the non-breeding season.

To examine the spatial distribution of the energy supply, we used the bioenergetics modeling results for the population objectives to estimate the contribution of each land cover type and each Central Valley basin to meeting the daily energy requirements. We summed the daily energy consumed in each land cover type ($EC_{i,t}$) to compare the cumulative total energy consumed in each land cover type over the course of the non-breeding season. Similarly, we estimated the proportion of the $EC_{i,t}$ consumed in each basin, based on the proportion of each land cover type in each basin, assuming no spatial variation in proportion open water or proportion accessible. We then summed the daily energy consumed in each basin across all land cover types to examine the daily energy consumed in each basin over the course of the non-breeding season.

Long-Term (100-Year) and Short-Term (10-Year) Habitat Objectives

We used the estimates of median S_t generated by the bioenergetics model to identify periods during the non-breeding season when meeting the long-term (100-year) population objectives requires additional shorebird foraging habitat (i.e., open water < 10 cm deep). For each of these shortfall periods, we calculated the median cumulative energy shortfall, and we used the estimates of mean energy density ($ED_{i,0}$) to generate a preliminary estimate of the corresponding area of additional shorebird foraging habitat that would be required to provide that amount of energy. However, a change in the distribution of energy across land cover types affects the distribution of energy consumed ($EC_{i,t}$) within the bioenergetics model, and thus the energy carried forward to the next time-step, which subsequently influences the estimated energy shortfalls in a non-linear way. Thus, we re-ran the bioenergetics model starting with the preliminary estimate of additional area needed, and iteratively tested higher and lower values to estimate the minimum area necessary to eliminate the energy shortfalls. To track progress toward these long-term habitat objectives, we then identified short-term (10-year) habitat objectives as 1/10th of the long-term objectives.

RESULTS

Population Objectives and Energy Needs

The observed size of the baseline shorebird community increased between August and April during the 1992-1995 baseline surveys (Figure 2A; Shuford et al. 1998), peaking during spring migration when shorebirds are concentrated in the Central Valley. Although the actual rate of change in the size of the shorebird community is unlikely to be linear throughout the non-breeding season, the sparse nature of the available data supported only a linear model. Consequently, the long-term (100-year) population objectives, based on doubling these observed population sizes, increase linearly from the assumed starting point of 50,000 birds on 1 July (CVJV 2006) to 269,143 by 15 August, reach a peak of 666,739 by 15 April, and then decline sharply back to 50,000 by 15 May (Figure 2A). These objectives are very similar to the objectives previously adopted in the Southern Pacific Shorebird Conservation Plan and the 2006 Central Valley Joint Venture Implementation Plan, which include 200,000 in the fall, 400,000 in the winter, and 600,000 in the spring (Hickey et al. 2003; CVJV 2006), but they provide specific numbers for each day of the non-breeding season.

The relative proportion of each species in the non-breeding shorebird community varied among the four survey periods (Shuford et al. 1998) such that the weighted average body mass of an individual

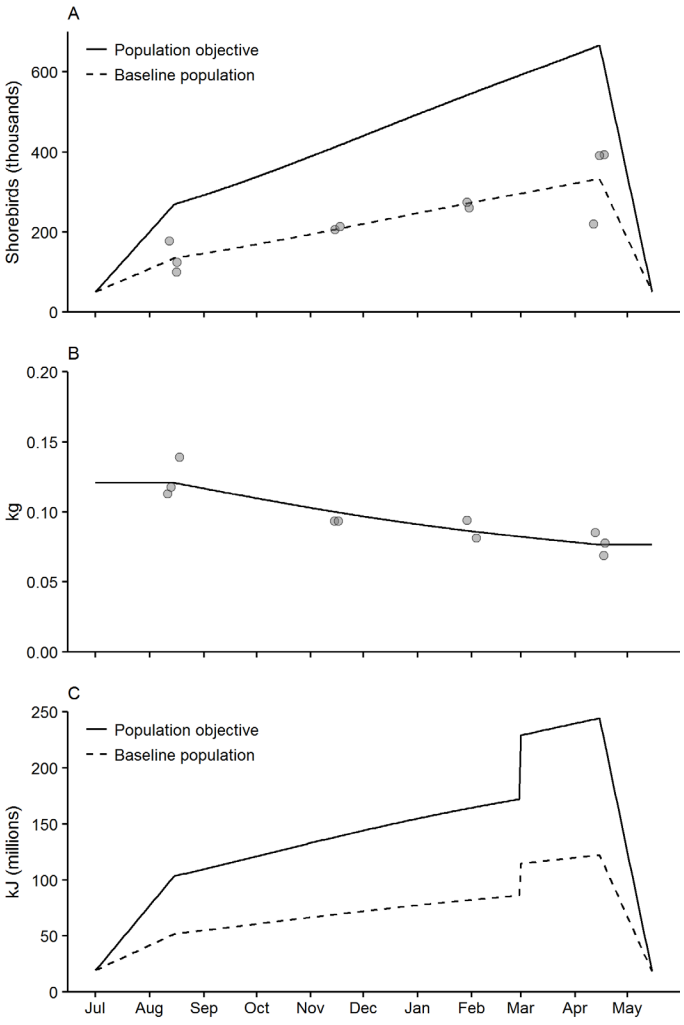

Figure 2 Central Valley Joint Venture non-breeding shorebird community estimated by (**A**) population sizes, (**B**) weighted average body mass, and (**C**) daily energy requirements. For (**A**) and (**C**), estimates are shown for the baseline population surveyed 1992–1995 (dashed) and for the long-term (100-year) shorebird population objectives (2× baseline; solid). For (**A**) and (**B**), points show the estimates from the individual baseline surveys (Shuford et al. 1998).

shorebird declined over the course of the season, from a peak of 121 g in August to 76 g in April (Figure 2B). Thus, based on allometric scaling equations, the average daily energy intake (*DEI*) of an individual shorebird would also be expected to decline. However, the size of the shorebird community increases over the course of the season, such that the net daily energy requirement (*DER*) of the entire shorebird community also increases over the course of the season (Figure 2C). After including a 33% increase in the *DER* to account for preparation for spring migration (CVJV 2006), there was a marked spike in DER from March through May.

Current Habitat Availability

Total Potential Habitat

The total extent of managed wetlands, rice, corn, and other crops varied among the eight planning basins (Table 3). Excluding Suisun basin, there are currently an estimated total of 74,835 ha (184,922 ac) of managed seasonal and semi-permanent wetlands in the Central Valley, with the largest extents in the San Joaquin, Butte, and Colusa basins (Figure 1). We estimated a 2007–2014 average of 219,082 ha (541,362 ac) of planted rice, which is located predominantly in the Sacramento Valley (northern) basins, and, after excluding corn grown in the San Joaquin and Tulare basins, we estimated a 2007–2014 average of 105,613 ha (260,976 ac) of planted corn, which is concentrated in the Delta basin. For the combined crop class of "other crops," we estimated an average of 830,293 ha (2,051,697 ac), which is concentrated in the Tulare basin.

Table 3 Estimated extent of potential habitat for non-breeding shorebirds in eight Central Valley Joint Venture planning basins (Figure 1; Suisun not included), shown in hectares (acres). Estimates include the estimated extent of wetlands in 2015 and the average extent of three crop classes, 2007–2014.

Basin	Wetlands	Rice	Corn	Other
Butte	15,015	54,850	3,006	11,215
Colusa	10,772	86,513	7,537	46,910
American	2,637	36,443	974	15,501
Sutter	1,460	28,533	1,978	11,905
Yolo	5,238	8,797	5,544	62,951
Delta	5,270	2,110	86,573	74,108
San Joaquin	24,786	1,836	—[a]	186,743
Tulare	9,659	0	—[a]	420,962
Total	74,835 (184,922)	219,082 (541,362)	105,613 (260,976)	830,293 (2,051,697)

a. We excluded the substantial amount of corn grown in the San Joaquin and Tulare basins, which is rarely flooded post-harvest.

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Proportion Open Water

The proportion open water varied considerably across land cover types and over the course of the non-breeding season (Figure 3). The predicted proportion of wetlands with open water peaked at 0.81 (95% CI: 0.76–0.86) by mid-January (Day 199) and had a relatively broad peak in comparison to rice, which reached an early-January peak of 0.69 (0.48–0.84; Day 188). The proportion of rice with open water reached a minimum in early April and then rose again as fields were again flooded for planting. Corn reached a peak of 0.22 (0.15–0.30) open water in early February (Day 223), and other crops had a relatively flat curve, with a predicted proportion open water of up to 0.03 (0.02–0.04). Multiplying the proportion open water by the total area of each land cover type, we estimated that the total area of potential shorebird habitat with open water peaked at 251,060 ha (620,381 ac) in early January (Day 192; Figure 4A).

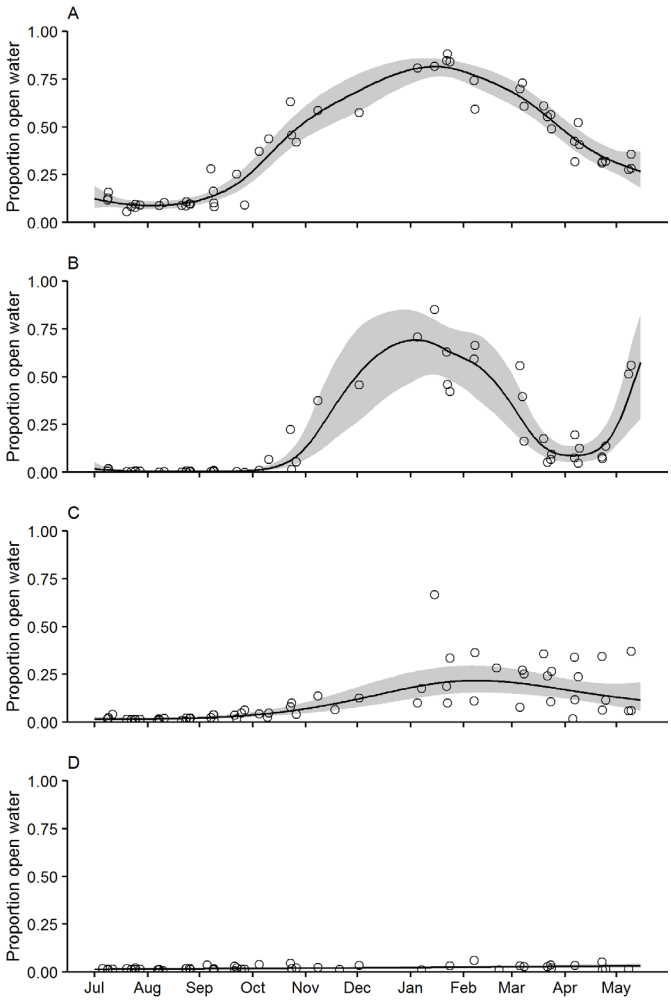

Figure 3 Temporal variation in the model-predicted proportion of four land cover types with open water in the Central Valley, 2007–2011: (**A**) managed wetlands, (**B**) rice, (**C**) corn, (**D**) other crops.

Proportion Accessible

The proportion of flooded rice fields that were of suitable depth for use by foraging shorebirds (<10 cm) was lowest in mid-winter, with a predicted value of 0.33 (0.09–0.71) when fields are fully flooded (Figure 5). The proportion accessible was highest at the start of fall flood-up (1 September) and after spring draw-down because very little area is flooded, and any water present is likely to be very shallow. The curve developed for seasonal wetlands by expert opinion was similar to rice, but with an

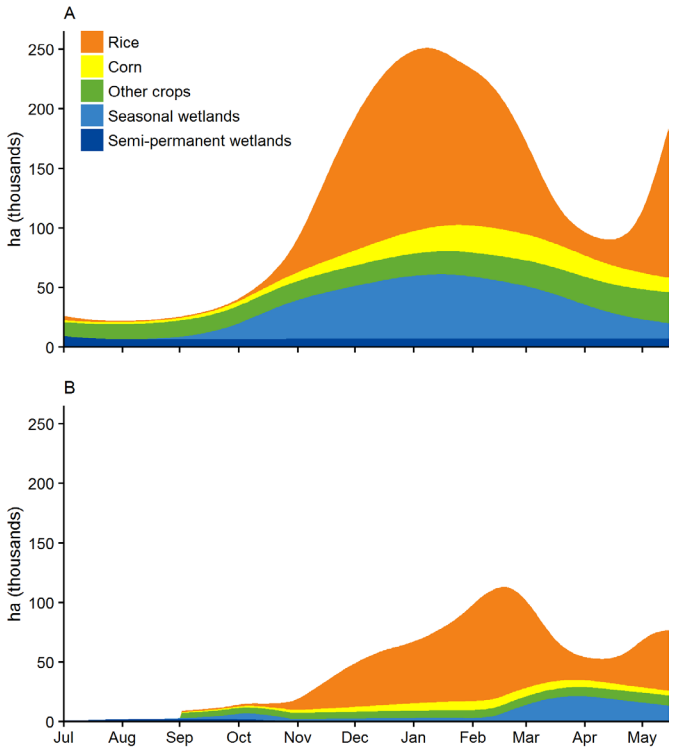

Figure 4 Temporal variation in the estimated total area of (**A**) open water and (**B**) open water accessible to shorebirds in the Central Valley by land cover type. Accessible open water includes open water <10 cm deep, but we also assumed no rice, corn, or other crops would be accessible to shorebirds before 1 September. Note the very small amounts of permanent/semi-permanent wetlands available in July and August.

earlier start to fall flood-up (1 August), and a lower estimated minimum of 0.05 during mid-winter (95% CI generated from logistic distribution with a scale of 0.25: 0.02–0.12). For permanent and semi-permanent wetlands, which remain fairly full year-round, the curve remained at 0.05 (0.02–0.12) most of the year, rising to 0.30 (0.15–0.52) during August and September when semi-permanent wetlands are drawn down. For corn and other crops, we applied the mean value of 0.33 (0.09–0.71) predicted for rice when fields are fully flooded.

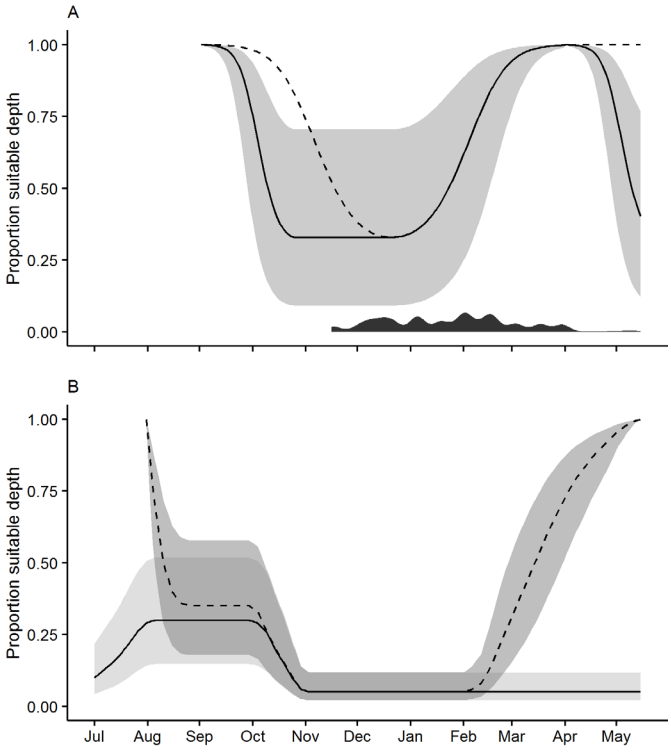

Figure 5 Temporal variation in the estimated proportion of rice fields and managed wetlands with open water that are accessible to non-breeding shorebirds in the Central Valley. (**A**) The proportion of flooded rice fields that are <10 cm deep by date, shown with 95% confidence intervals and the relative distribution of sampling data at the bottom in dark gray. Because of a lack of data during the fall, the dashed line shows the model-predicted symmetrical curve, and the solid line is the final adjusted curve with double the rate of change during fall flood-up (solid). We assumed no rice would be accessible to shorebirds before 1 September. (**B**) The proportion of managed wetlands that are <10 cm deep by date, derived from expert opinion and separated by seasonal wetlands (solid) and permanent or semi-permanent wetlands (dashed). Also shown are the estimated confidence intervals generated from a logistic distribution with scale of 0.25. We assumed there would be no open water in seasonal wetlands before 1 August.

Multiplying the daily mean estimates of proportion accessible by the daily mean estimated total area of each land cover type with open water (Figure 4A), we estimated the temporal variation in the total area of accessible open water foraging habitat for shorebirds (Figure 4B). We estimated that accessible foraging habitat reached, on average, a peak of 113,006 ha (279,244 ac) in mid-February (Day 232), over a month later than the peak of open water, but would rise again in late-April and May as rice fields are again flooded for planting (Figure 4B).

Current Energy Density

The five Central Valley studies provided 82 estimates of benthic invertebrate biomass density (kg ha^{-1}) and energy density (MJ ha^{-1}) from managed wetlands and 76 from flooded rice. A broad range of benthic invertebrate taxa were represented, with estimated average individual biomass ranging 0.003–2.3 mg and estimated mean energy content ranging 9.13–25.60 MJ kg^{-1} (Appendix A). We found strong support for a difference between wetlands and rice in both mean biomass density and mean energy density (both Akaike weights = 0.78), with higher estimates of each in wetlands (Figure 6). The model-averaged predicted mean biomass density in rice was 4.9 kg ha^{-1} (95% CI: 3.0–7.9 kg ha^{-1}) and in wetlands was 9.0 kg ha^{-1} (4.5–18.1 kg ha^{-1}), both lower than the estimate of 20 kg ha^{-1} previously adopted by the CVJV which was based on estimates from the Mississippi Alluvial Valley (Loesch et al. 2000; CVJV 2006). The model-averaged predicted mean energy density in rice was 104.9 MJ ha^{-1} (66.6–165.4) and in wetlands was 186.6 MJ ha^{-1} (97.9–355.5).

Bioenergetics Model

Baseline Population

After accounting for dynamic habitat availability and consumption of food resources in each time-step, the total energy accessible (TEA_t) to shorebirds in the Central Valley at the baseline population size reached a peak in mid-February (Day 232; Figure 7A), at the same time as the peak in accessible

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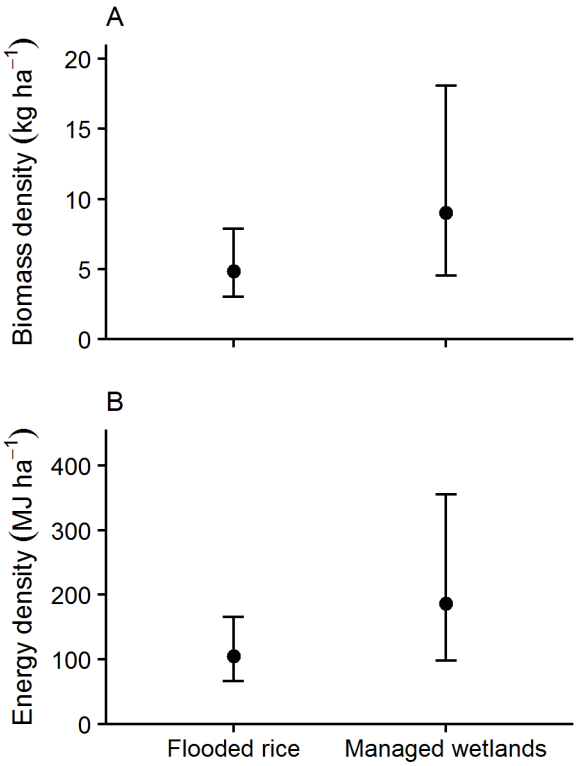

Figure 6 Estimates of model-averaged predicted (**A**) mean biomass density (kg ha^{-1}) and (**B**) mean energy density (MJ ha^{-1}) in Central Valley managed wetlands and flooded rice, shown with 95% confidence intervals.

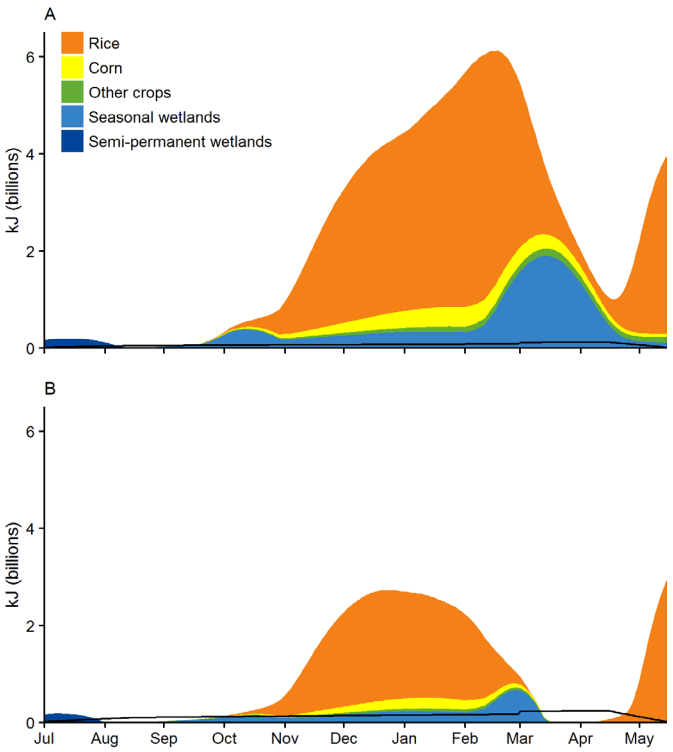

Figure 7 Estimated median accessible energy contributed by each land cover type in the Central Valley after accounting for energy consumption during previous time steps at (**A**) the baseline population size (1992–1995) and (**B**) the population objectives (2x baseline). The solid line shows the daily energy requirement of the shorebird community for comparison.

habitat (Figure 5)—and just before the daily energy requirement rises by 33% as birds prepare for spring migration. The median peak value was 6.32 billion kJ (95% CI: 2.62–12.91), but this energy stockpile was rapidly drawn down during March and April as flooded rice and seasonal wetlands began to dry out (Figure 3) while the daily energy requirements (DER_t) of shorebirds continued to rise (Figure 2C). The subsequent increase in energy accessible in late April and May reflects both a reduction in the population size and daily energy requirements of shorebirds, and spring flooding in rice fields for planting. Energy accessible to shorebirds was lowest during mid-August (Day 48; 0.02 billion kJ, 95% CI: 0.00–0.31), when shorebirds must rely primarily on wetlands (Figure 7A). The daily energy requirement on Day 48 is 0.05 billion kJ, generating an estimated energy shortfall. The median daily energy shortfall (S_t) rose above 0 from early August through early September (Days 40–72), although the 95% confidence intervals extended above 0 from late July through late September (Days 23–88) and again in April (Days 278–297; Figure 8A). Thus, the bioenergetics model suggests that current habitat availability and management practices may fall short in August and September, but on average appear sufficient to meet the daily energy requirements of the baseline population size during the rest of the non-breeding season.

Population Objectives

With the shorebird community at the size of the population objectives (i.e., double the baseline population), the energy accessible was consumed much more rapidly throughout the non-breeding season. Consequently, the total energy accessible (TEA_t) was lower during the fall and reached a much lower median peak value of 2.81 billion kJ (95% CI: 0.72–8.33) almost 2 months earlier than

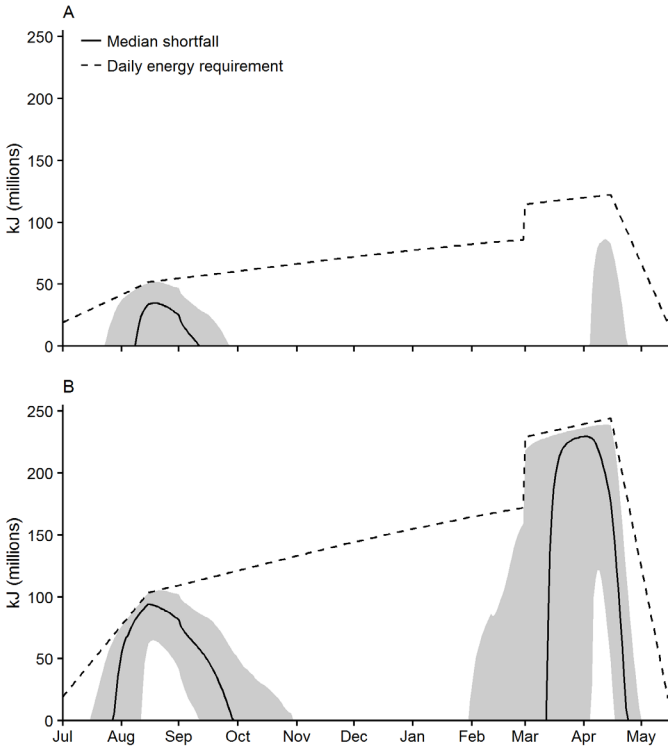

Figure 8 Median shortfalls (solid line) in meeting the daily energy requirements (dashed line) of the non-breeding shorebird community at (**A**) the baseline population size (1992–1995) and (**B**) the population objectives (2x baseline). Shown with 95% confidence intervals.

for the baseline population, in late December (Day 175; Figure 7B). As the daily energy requirement continued to rise through the spring, the accessible energy supply was even more rapidly depleted, reaching a minimum value of 0.01 billion kJ (95% CI: 0.00–1.03) in late March (Day 273). The fall minimum occurred in early August (Day 41) at 0.01 billion kJ (95% CI: 0.00–0.12). The median daily energy shortfall (S_t) was greater than 0 during two corresponding periods of the year, late July through September (Days 28–90) and mid-March through late April (Days 256–297; Figure 8B), while the 95% confidence intervals extended above 0 from mid-July through October (Days 16–122) and again from late January through April (Days 215–304). Thus, the bioenergetics model suggests that current habitat availability is not sufficient to meet the daily energy requirements of the shorebird community at the size of the population objectives during the fall and spring.

Wetlands Minimum

We found that wetlands were not sufficient to meet the CVJV's goal that wetlands supply at least 50% of the daily energy requirement during October–February and 100% of the daily energy requirement in July–September and March–May. For both the baseline population and the population objectives, median S_t extended above 0 in the fall and spring (Figure 9). For the population objectives, the median S_t matched the wetlands daily energy requirement from March through May, indicating that all energy accessible in wetlands would be consumed and no longer available late in the non-breeding season. The timing and magnitude of the energy shortfalls in meeting the wetlands requirement generally agreed with the timing and magnitude of the overall shortfalls in meeting the daily energy requirements (Figure 8), suggesting that both could be addressed by providing additional shorebird foraging habitat in wetlands during the fall and spring.

Energy by Land Cover and Basin

For the population objectives, we estimated that seasonal and semi-permanent managed wetlands would together contribute a median of 33% (95% CI: 21%–49%) of the cumulative total energy consumed over the non-breeding season (Figure 10A). Rice contributed 56% (41%–68%), and corn and other crops contributed the remainder, with 7% (4%–12%) and 4% (1%–7%), respectively. Consequently, we estimated that basins with the largest area of wetlands and rice would contribute larger proportions of the energy consumed (Figure 10B). We estimated that Colusa basin would contribute the most, with a median of 28% (95% CI: 24%–31%) of the energy consumed, followed by the Butte (21%, 20%–22%) and San Joaquin (12%, 9%–17%) basins.

Model Sensitivity

We found that the precision of the bioenergetics modeling results was most sensitive to the uncertainty in our estimates of energy density ($ED_{i,0}$) in wetlands and rice (Figure 11). The cumulative total S_t differed by 11.77 billion kJ in wetlands and 9.21 billion kJ in rice solely because of varying energy density estimates between the lower and

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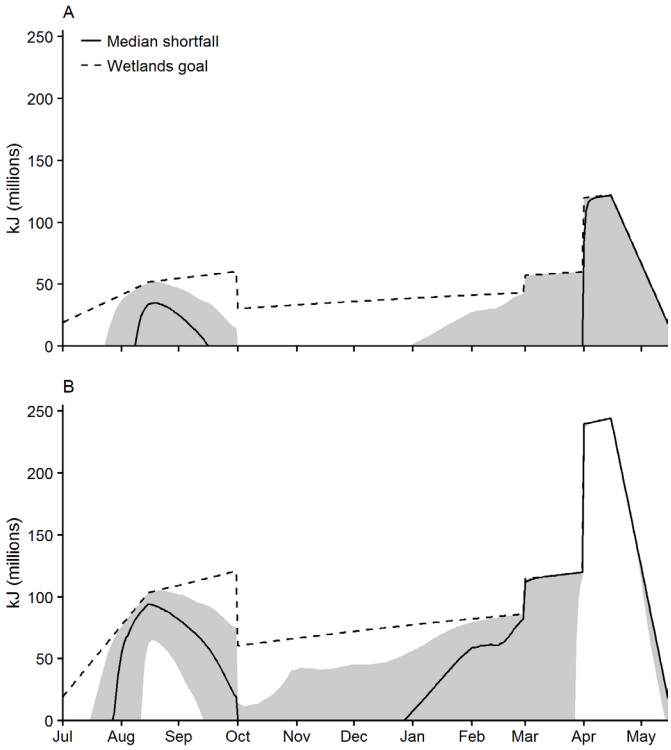

Figure 9 Median shortfalls (solid line) in meeting the wetlands goal (dashed line) of supplying 50% of the daily energy requirements for non-breeding shorebirds in the Central Valley during October–March and 100% in July–September and April–May at (**A**) the baseline population size (1992–1995) and (**B**) the population objectives (2x baseline). Shown with 95% confidence intervals.

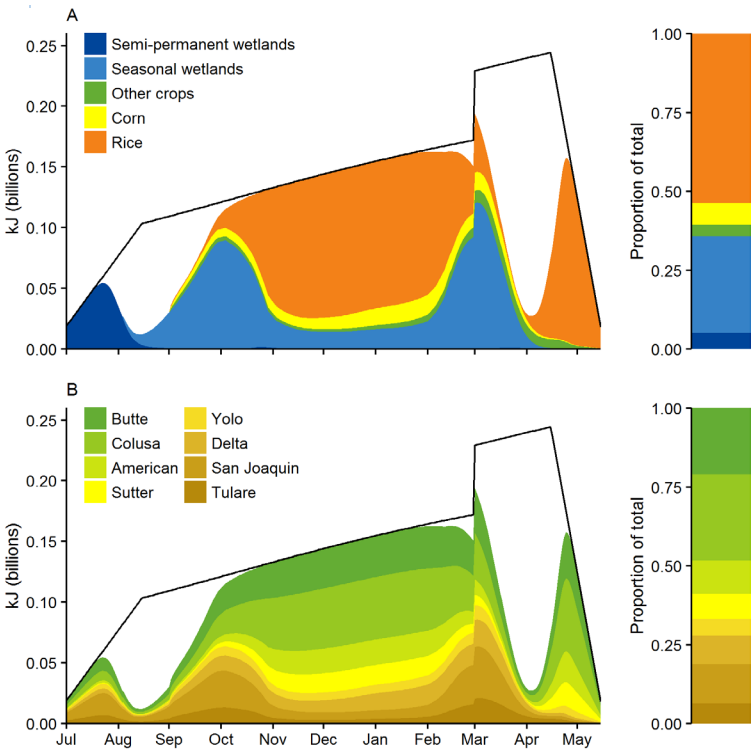

Figure 10 Estimated median energy consumed by non-breeding shorebirds in (**A**) each land cover type and (**B**) each Central Valley Joint Venture basin over the course of the non-breeding season, shown with the proportion of the cumulative total. The solid line shows the daily energy requirement of the shorebird community for comparison.

upper 95% confidence limits (Figure 6). Although we assumed energy density in corn and other crops was the same as in rice, the model was much less sensitive to the uncertainty in the energy density of these crops, with cumulative total S_t differing by 0.90–1.45 billion kJ. Similarly, the model was less sensitive to the uncertainty in our estimates of proportion open water ($PF_{i,t}$), ranging from 0.84 to 6.34 billion kJ depending on the land cover type, and uncertainty in proportion accessible ($PA_{i,t}$), ranging from 0.04–0.63 billion kJ.

Long-Term and Short-Term Habitat Objectives

Meeting the daily energy requirements of the long-term (100-year) population objectives will require eliminating the projected energy shortfalls. During the fall (late July through late September), a cumulative total of 4.02 billion additional kJ (95% CI: 2.23–5.83) are needed to meet the population objectives, and, during the spring (mid-March through late April), a cumulative total 7.79 billion additional kJ (95% CI: 2.00–14.14) are needed. Because energy density estimates were higher in wetlands (Figure 6) and because there were shortfalls in meeting the goal for energy supplied by wetlands, we estimated long-term habitat objectives as the minimum area of additional shorebird foraging habitat in wetlands (i.e., open water <10 cm deep) required to eliminate these energy shortfalls, defined as all median $S_t = 0$. Assuming no change to the benthic invertebrate energy density in wetlands (Figure 6B), and no losses of existing shorebird foraging habitat in wetlands or post-harvest flooded crops (Figure 4B), we estimated that eliminating the energy shortfalls will require 21,598 ha (53,370 ac) of additional shorebird foraging habitat maintained

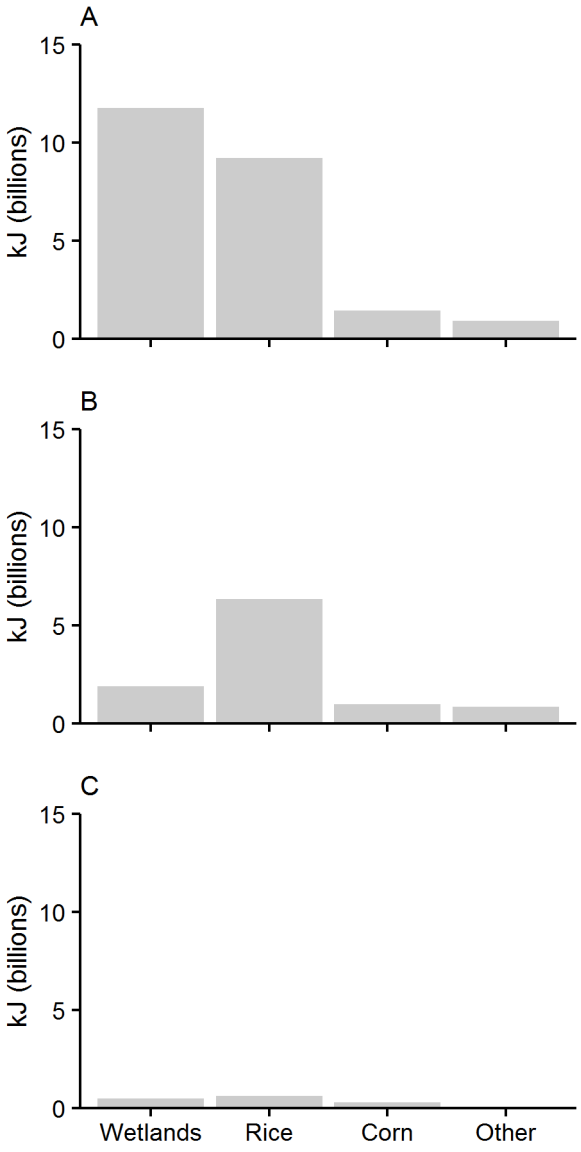

Figure 11 Sensitivity of the bioenergetics modeling results to uncertainty in (A) energy density, (B) proportion open water, or (C) proportion accessible in each land cover type. Sensitivity is presented as the difference in the estimated total energy shortfall (kJ) resulting from varying one parameter in one land cover type between its lower and upper confidence limits.

from late July through September and 46,920 ha (115,942 ac) maintained from mid-March through late April in the Central Valley. The corresponding short-term (10-year) habitat objectives (one-tenth of the long-term habitat objectives) are to add 2,160 ha (5,337 ac) and 4,692 ha (11,594 ac) of shorebird foraging habitat during these respective periods.

DISCUSSION

Central Valley wetlands and flooded agriculture are recognized as sites of international importance to shorebirds (WHSRN c2009). Here, we have built on the CVJV's bioenergetics modeling approach to identify the timing and magnitude of limitations in wetland foraging habitat during the non-breeding season (CVJV 2006), and have estimated the amount of additional habitat that would be needed to meet the long-term goal of doubling the baseline population size. Protecting, restoring, and managing Central Valley wetlands to support non-breeding shorebirds will benefit shorebird populations well beyond the Central Valley, including several species of conservation concern (Table 1). Further, wetlands provide habitat for other animals and plants that together benefit the people of the Central Valley in many ways. The ecological benefits include reduction of flood risk, improvement of air and water quality, groundwater recharge, and carbon sequestration (Finlayson et al. 1999; Zedler and Kercher 2005). The sociological benefits include increasing property values, providing recreational opportunities, and attracting wildlife watchers and hunters who help support local economies (Carver 2013; Carver and Caudill 2013; Liu et al. 2013).

Measuring Success

The contribution of individual wetland restoration and management efforts to achieving the short-term (10-year) and long-term (100-year) habitat objectives can be estimated as the increase in accessible (<10 cm deep) open water area maintained throughout the energy shortfall periods in fall and spring. Meeting the long-term habitat objectives likely requires a combination of (1) the restoration of additional wetlands, (2) increasing the existing area that has open water during the shortfall periods, such as by earlier flooding of seasonal wetlands in the fall or by delaying, slowing, or staggering draw-downs of semi-permanent wetlands in the fall and of seasonal wetlands in the spring (Figure 3; Colwell et al. 1995), or (3) increasing the proportion of the open water area in wetlands and flooded agriculture that is <10 cm deep (Figure 5), such as by reducing overall water depth or creating wetlands with more topography and gradually sloped edges

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(Taft et al. 2002; Reiter et al. 2015b). However, changes in habitat availability during one part of the season can affect energy availability later in the season in unexpected and non-linear ways, such that a 50% increase in available habitat does not necessarily correspond to a 50% decrease in energy shortfalls. For example, if all seasonal wetlands were maintained <10 cm deep throughout the non-breeding season, the energy supplied by seasonal wetlands would be depleted more rapidly, resulting in spring energy shortfalls that are actually larger than the current energy shortfall estimates (Appendix B). Consequently, to identify the most effective strategies to meet the energy shortfalls, we recommend using the bioenergetics model to examine the outcomes of changes in the extent, timing, or depth of managed wetlands and post-harvest flooded crops.

An alternative, complementary approach would be to identify and implement management actions that enhance the benthic invertebrate production and energy density in wetlands and post-harvest flooded agriculture, reducing the total area of shorebird foraging habitat required. For example, invertebrate productivity can be affected by vegetation composition and cover, topography and water depth diversity, duration of flooding, and salinity (Severson 1987; Batzer and Resh 1992; Batzer and Wissinger 1996; Takekawa et al. 2006; Batzer 2013). However, invertebrate responses to management may be taxon- and region-specific, requiring careful research to identify effective strategies (Batzer 2013). In addition to tracking efforts to address the energy shortfalls, measuring success will require monitoring changes in habitat availability and the size of the non-breeding shorebird community over time to gauge progress toward achieving the short- and long-term habitat and population objectives.

We set population objectives based on doubling the baseline population size of shorebirds throughout the Central Valley, but the relative abundance of individual species and available habitat varies by planning basin (Figure 1; Shuford et al. 1998). Thus, we recommend that wetland restoration and management efforts are distributed across the Central Valley such that habitat is available for shorebirds throughout the Central Valley over the entire non-breeding season. This approach will increase the likelihood that all shorebird species in the Central Valley—as well as people in communities throughout the Central Valley—benefit from these efforts. Further, distributing habitat across the Central Valley limits reliance on a single area, allows wildlife to select habitat from a broader range of environmental conditions (e.g., climate conditions, predator abundance, or anthropogenic disturbance), and builds in redundancy that would increase the resilience of shorebird populations and wetland ecosystem services to environmental disasters in one part of the Central Valley (Redford et al. 2011; Biggs et al. 2012).

Research Needs

As we anticipated from prior work (CVJV 2006), we identified energy shortfalls during the fall (August–September) and spring (late February–May). However, several sources of uncertainty limited the precision of our energy shortfall estimates (Figure 8). The model's results were most sensitive to the uncertainty in our energy density estimates, an area that has been previously identified as a major source of uncertainty in bioenergetics modeling (Williams et al. 2014), suggesting that research in this area would be particularly valuable in improving our understanding of energy shortfalls. Recent data on benthic invertebrate energy density in each land cover type are limited, as is information about any spatio-temporal variation in energy density and growth rates over the non-breeding season. Invertebrate growth rates may be low during the winter because of colder temperatures and higher during the fall and spring (Duffy and LaBar 1994), but given the considerable uncertainty in these growth rates and to remain conservative in our estimate of energy supply, we assumed any growth was negligible. We also assumed there was no other energy supply available to shorebirds outside of wetlands and flooded agriculture, although some may forage in upland habitats (Shuford et al. 2013). Thus, the energy shortfalls and habitat objectives may be over-estimated, and, as more information about benthic invertebrates or any of the other model parameters becomes available, our bioenergetics model can be updated and the habitat objectives can be refined.

We also assumed an ideal free distribution (Fretwell and Lucas 1969) of shorebirds across all available habitat throughout the Central Valley and our

bioenergetics model did not explicitly consider the spatial distribution of the available habitat during each time-step. Shorebird preferences for foraging in certain land cover types or areas of the Central Valley, such as because of proximity to cover for predators or preferred roost sites (Fuller et al. 2013; Santiago–Quesada et al. 2014) or spatial variation in preferred prey availability (Alves et al. 2013), could cause energy availability to be depleted in preferred areas more quickly than we estimated. Similarly, a concentration of molting birds in one area or a pulse of migrating birds passing through could cause energy availability to be depleted in those areas more quickly. In addition, shorebirds may abandon available habitat once prey availability is reduced below a certain density (Bedoya–Perez et al. 2013). Further, if some of the available habitat during any time-step is located far away from the majority of available habitat, shorebirds may not locate it or may require more energy to reach it. Alternative approaches, such as agent-based models (e.g., Stillman and Goss–Custard 2010; Miller et al. 2014), track individual behavior and spatially explicit habitat availability, including changes in energy requirements resulting from increased travel time between foraging and roosting areas. However, these approaches require an additional level of parameterization to model the behavior of individuals of each species and their habitat-selection processes, as well as the spatial distribution of available habitat during each time step, which we were not able to address at this time.

Our estimates of the additional shorebird foraging habitat required to meet the long-term population objectives also assume that none of the currently available foraging habitat will be lost, and there will be no changes in shorebird energy requirements or the energy density of managed wetlands or flooded agricultural fields. However, climate change may result in long-term changes to all these parameters. For example, the abundance, composition, and daily energy requirements of Central Valley non-breeding shorebirds could all be affected by warmer winter temperatures, which may induce shifts in winter ranges, changes in migration timing, and a reduction in the energy cost of thermoregulation in winter (Bairlein and Hüppop 2004). Climate change may also affect energy supply through changes in benthic invertebrate composition (Burgmer et al. 2007). Further, long-term changes in water policies or greenhouse gas emissions policies in response to climate change can significantly affect wetlands, the total area of suitable crop classes planted, and whether crops will continue to be regularly flooded post-harvest (Hanak and Lund 2012; Petrie et al. 2016; Sesser et al. 2016). The ongoing drought in California led to a 23% decline in planted rice between 2013 and 2014, and an additional 5% decline between 2014 and 2015, resulting in the smallest extent of planted rice since 1992 (USDA c2016). Projected changes in temperature and hydrology from climate change (Thorne et al. 2015), sea level rise in the Delta (CNRA 2009), and expansion of urban areas throughout the Central Valley (Landis and Reilly 2003) could all affect the total area of suitable crop classes and the availability of water for managed wetlands and post-harvest flooding. Similar effects of climate change around the world may also have long-term effects on global and regional markets, affecting, in turn, how much of a particular crop is grown in the Central Valley (Hatfield et al. 2014). Thus, we recommend using the bioenergetics model to evaluate the effects of future scenarios on shorebirds, and adjust conservation objectives or restoration and management strategies accordingly. We also recommend that shorebird conservation efforts seek to increase support for climate-smart wetland restoration and management projects that will continue to provide multiple benefits for Central Valley ecosystems and communities.

CONCLUSIONS

The Central Valley's existing network of restored and managed wetlands and post-harvest flooded agriculture provides substantial foraging habitat for migrating and wintering shorebirds, but habitat remains limited during the fall and spring, and we estimated that wetlands would contribute only 33% of the total energy required to meet the long-term population objectives. By creating additional wetlands, and increasing the proportion of managed wetlands that have shallow open water during the fall and spring, we estimated that the Central Valley could support double the baseline population size while reducing reliance on flooded agriculture,

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which would benefit shorebird conservation and provide multiple benefits to people in communities across the Central Valley. However, there remains considerable uncertainty surrounding the extent of habitat required to achieve the population objectives, especially spatio-temporal variation in the benthic invertebrate energy supply and the effects of climate change. As additional information becomes available, our bioenergetics modeling approach will provide a transparent, repeatable process for identifying the timing and magnitude of habitat needs, exploring the effects of changes in habitat availability, and identifying the most efficient strategies for achieving conservation objectives.

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