

ARTICLE

Shorebird food energy shortfalls and the effectiveness of habitat incentive programs in record wet, dry, and warm years

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Abstract

Programs that incentivize private landowners to create habitats that offset losses due to conversion and climate change are increasingly being used to bolster sensitive wildlife populations. In the Central Valley of California, shorebird habitat incentive programs pay landowners to create additional habitat during the non-breeding season by flooding their fields. However, it remains unclear how successful these programs have been in supporting baseline shorebird population needs or meeting established population goals, particularly in the face of changing environmental conditions. To address these questions, we used bioenergetics modeling to estimate shorebird food energy needs over four consecutive years that had the highest annual mean air temperatures ever recorded in California, and included years of extreme drought, as well as the second wettest winter on record. Our objectives were to (1) characterize annual variability in the timing and magnitude of shorebird food energy shortfalls, (2) estimate the contributions that incentive programs made to meeting these needs, and (3) develop recommendations for implementation of future habitat programs to advance shorebird conservation in the region. Overall, we found a high level of consistency in the timing and magnitude of habitat shortfalls, especially in fall, despite large differences in annual rainfall, a result that was unexpected, but that emphasizes how highly managed the hydrological system is in the Central Valley. We also found that the magnitude of both fall and spring energy shortfalls increased, relative to recent (2007–2014) estimates, perhaps due to aberrantly warm conditions. Incentive programs implemented to provide supplemental habitat were somewhat effective in reducing shortfalls for the assumed baseline population, but there were consistent unmet habitat needs when there were not enough shallow open water foraging areas available. Strategies to offset these remaining food energy deficits include scaling up habitat investments, adjusting the timing of habitat programs to better match the migration patterns of the birds, and adapting

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programs to new geographies. To the extent that there is variability in annual habitat need we recommend implementing a dynamic conservation approach. This involves scaling the amount of additional habitat created to match the shifting needs of the birds to maximize return on investment.

KEYWORDS

agri-environment scheme, bioenergetics, California, Central Valley, drought, dynamic conservation, habitat deficit, Pacific Flyway, payment for ecological services, rice, shorebird, wetland

INTRODUCTION

Creating temporary habitat on working lands is becoming increasingly important for meeting the habitat needs of migratory species that have lost natural habitats due to conversion (Mora & Sale, 2011; Runge et al., 2015). However, knowledge of where, when, and how much habitat is required to support target populations is needed for this strategy to be effective and efficient in allocating limited resources (Evans & Green, 2007; Reynolds et al., 2017). In highly dynamic systems, it may be hard to predict how much habitat will be available at any point in time, and hence how much additional habitat is needed to meet conservation goals (Moilanen et al., 2014). Such is the case with wetlands in California's Central Valley, where there is high and increasing annual variability in rainfall (He & Gautam, 2016), ~90% of the historical wetlands have been lost (Frayer et al., 1989; Dahl, 1990), and waterbirds depend on a combination of refuges, private managed wetlands, and intentionally flooded agricultural fields (Dybala et al., 2017; Stralberg et al., 2011). Furthermore, future projections suggest that interannual variability in the amount of waterbird habitat may increase with time due to complex interactions of climate and human water management, even if long-term declines in average precipitation are not substantial (Matchett & Fleskes, 2017). Already we have seen that the extent of flooded habitat available to shorebirds can decline by as much as 80% between wet and dry years (Reiter, Elliott, et al., 2015).

In response to the overall loss of wetland habitat in the Central Valley, and the desire to compensate for recent drought conditions, several shorebird habitat incentive programs have been established to pay private landowners to flood their fields and create additional shorebird habitat during migration and overwintering when habitat is thought to be in short supply (MBCP, 2014; Reynolds et al., 2017; Strum et al., 2013). These incentive programs have successfully enrolled thousands of hectares each year, and during certain time periods, have provided a large proportion of the total flooded

habitat available to shorebirds in the Central Valley (Reiter et al., 2018). Program fields have proven to be effective in attracting large numbers of shorebirds (Golet et al., 2018; Sesser et al., 2018); however, it remains unclear what their contribution has been to meeting recently established habitat conservation objectives developed by the Central Valley Joint Venture (for the non-breeding season (CVJV, 2020)). The CVJV is a coalition of State and Federal agencies, private conservation organizations and a corporation working to provide habitat for migrating and resident birds in the Central Valley. Furthermore, it is unknown how incentive program contributions vary across years, and to what extent there are unmet habitat needs. The CVJV shorebird habitat objectives were developed using a bioenergetics approach that examined average annual habitat conditions (2007–2014) to identify times of the year when energy demands of the target population size exceeded available food resources (Dybala et al., 2017). This comparison of demands and availability of food energy provided estimates of the timing and amount of additional habitat that is needed on average but did not evaluate the extent to which these factors varied across years. Thus, it remains unclear whether and how much additional habitat is needed when conditions change, such as during extreme drought.

In this study, we used the Dybala et al. (2017) bioenergetics model to estimate shorebird habitat availability and needs in each of four consecutive years, including years of extreme drought and the second wettest winter on record. Similar bioenergetic approaches have been used to assess food resources for overwintering and migrating waterfowl in the Pacific (CVJV, 2020) and Central Flyways (Schepker et al., 2019) under differing habitat availability scenarios, including drought (Petrie et al., 2016). The objectives of our study were to (1) characterize the annual variability in the timing and magnitude of shorebird habitat needs, (2) estimate the contributions that incentive programs made to meeting these needs, and then (3) apply these results to develop recommendations for implementation of future habitat programs to advance shorebird conservation in the Central Valley.

METHODS

Study area

The focal area for this study was the Central Valley of California as defined by the Central Valley Joint Venture. This area is entirely within the Great Valley ecoregion (Hickman, 1993), and extends >400 km north to south, up to 100 km east to west, and is bounded by the Sierra Nevada, Cascade, and California Coast Range mountains (see figure 1 in Dybala et al., 2017). The area is one of the most productive agricultural regions in the world and is a major migratory stopover and wintering site along the Pacific Flyway that is of hemispheric importance to waterbirds (CVJV, 2020; Gilmer et al., 1996; Shuford et al., 1998). Approximately 3 million dabbling ducks, 2 million geese, and 500,000 shorebirds use the Central Valley each year (Collins et al., 2011; Shuford et al., 1998). In fall, Great Salt Lake is the only inland site in western North America with consistently greater shorebird numbers (Shuford et al., 1998).

With most naturally occurring wetlands in the Central Valley gone, agricultural crops that are flooded post-harvest and hydrologically managed wetlands are the primary habitats for migratory shorebirds (Dybala et al., 2017; Elphick & Oring, 1998). Currently, there are ~75,000 ha of managed wetlands in the Central Valley (Dybala et al., 2017), one-third of which are publicly owned (CVJV, 2020). The main agricultural crops that provide shorebird habitat include post-harvest flooded rice and corn and, in lesser amounts, other row and field crops when they are flooded. Flooded rice and corn fields provide valuable food resources, including leftover rice grain and invertebrates, and are used by over 50 waterbird species (Elphick & Oring, 1998; Eadie et al., 2008; Shuford et al., 2019), including several that have special conservation status (Elphick & Oring, 1998; Shuford & Gardali, 2008).

The Central Valley has a Mediterranean climate with hot, dry summers and cool, variably wet winters. Most of the water that is used to provide initial flooding of seasonal waterbird habitat comes from storage reservoirs that capture runoff from mountain rainstorms and melting snowpack (Carle, 2009). An elaborate system of dams, canals, and water control structures is used to capture and distribute water in accordance with existing water rights (Hanak & Lund, 2012), but even so shortages often occur for both people and nature. Habitat availability is thus dynamic within and among years and highly dependent on management (Reiter, Elliott, et al., 2015; Reiter et al., 2018; Schaffer-Smith et al., 2017).

During the four years of our study (2014–2017) the Central Valley experienced greatly varying hydrologic

conditions. The first two water years (WYs 2014 and 2015), which ran from the previous October through September, were classified as “critically dry” in both the northern and southern portions of the Central Valley, areas known as the Sacramento Valley and San Joaquin Valley, respectively. The severe drought continued through February 2016, but then significant rains fell such that WY2016 ended up as “below normal” in Sacramento Valley and “dry” in San Joaquin Valley. In striking contrast to the earlier years, WY2017 was the second wettest year on record across the Central Valley and was classified as “wet” in both Sacramento and San Joaquin valleys (DWR 2018).

Because seasonal rains in the Central Valley do not typically come until October, the start of the fall non-breeding season for shorebirds (defined as 1 July) was primarily influenced by the hydrologic conditions of the previous winter (Reiter, Elliott, et al., 2015; Reiter et al., 2018), and thus the previous water year. However, during the remainder of the non-breeding season including spring migration, rainfall patterns had a pronounced effect on habitat availability (Golet et al., 2018; Schaffer-Smith et al., 2017).

Incentive programs

The three landowner habitat incentive programs that we evaluated included The Nature Conservancy’s BirdReturns program (Golet et al., 2018; Reynolds et al., 2017), and two Natural Resources Conservation Service (NRCS) Waterbird Habitat Enhancement Program (WHEP) practices (MBCP, 2014; Sesser et al., 2018). BirdReturns had separate spring and fall enrollment periods, while the NRCS program had two different practices for what roughly corresponded to these same time periods: WHEP Fall Flooding (Practice 644C, “Seasonal flooding with gradual drawdown”) and WHEP Variable Drawdown (Practice 644A “Winter Flooding with Variable Drawdown”). The field and flood management practice requirements were broadly similar across programs and all focused on providing high-quality habitat for shorebirds, primarily in harvested or fallow rice fields (Table 1). Although the enrollment period for WHEP Variable Drawdown started in November, shorebird accessible habitat was only provided during the drawdown stage between 1 February and 28 February, with a few enrollments that delayed their initial drawdown going somewhat later.

Of all the programs, WHEP variable drawdown had the greatest total area enrolled each year, although it decreased in the latter two years of the study (Table 2) because of funding appropriation schedules at NRCS. High overall enrollment in this program was likely due

TABLE 1 Field and flood management practices for shorebird habitat incentive programs.

Incentive program	Required practices ^a	Enrollment dates	Enrollment options
BirdReturns fall	Fields $\geq 75\%$ flooded, ≤ 10 cm deep	Between 15 August and 28 October	2- or 4-week options
WHEP Fall Flooding	Fields initially flooded 5–10 cm deep for 14 days. Then gradually drained over the subsequent 14 days.	Between 1 July and 28 September	Any consecutive 28-day period
BirdReturns spring	Fields $\geq 75\%$ flooded, ≤ 10 cm deep.	Between 1 February and 14 April	2-, 4-, 6-, 8-, or 10-week options
WHEP Variable Drawdown	Fields initially flooded ≥ 15 cm deep then 25% drained for four subsequent weeks.	Initial flood-up between 1 November and 15 December. Drawdowns initiated 1 February	None

^aAll programs also required rice stubble, if present, to be substantially incorporated into the soil.

Note: WHEP, Waterbird Habitat Enhancement Program.

TABLE 2 Total areal extent (ha) enrolled in each incentive program.

Date	BirdReturns		WHEP		Total
	Fall	Spring	Fall Flooding	Variable Drawdown	
2013–2014	0	5113	104	23,940	29,157
2014–2015	2565	1643	138	26,587	30,933
2015–2016	2824	2830	19	14,372	20,045
2016–2017	1749	1340	162	7603	10,853

to the timing being highly compatible with the rice production schedule, with no requirement for late spring flooding. In contrast, the WHEP Fall Flooding practice, which overlapped significantly with the rice production phase, always had small enrollment, and typically was implemented on fields that had not been planted with rice in the preceding growing season.

Bioenergetics model

To estimate the impacts of incentive programs on the timing and magnitude of shortfalls in the food energy available to non-breeding shorebirds, we applied a previously developed bioenergetics model that compares the daily energy needs of the shorebird community against the daily energy supply available from suitable foraging habitat (Dybala et al., 2017). This approach required first estimating the total amount of suitable foraging habitat available to shorebirds throughout each of the four non-breeding seasons studied (1 July through 15 May 2013–2014, 2014–2015, 2015–2016, and 2016–2017). These years were selected for study because they were the first to include both spring and fall habitat programs. Habitat availability typically varies throughout the non-breeding season due to changes in the timing, extent, and depth of

open water in managed wetlands and croplands (Dybala et al., 2017), and we also expected it to vary across years due to differences in water year types and variation in incentive program participation.

Annual and temporal availability of non-incentivized habitat

Land cover types that are potentially suitable habitat for non-breeding shorebirds include both managed wetlands and crops that are regularly flooded post-harvest, such as rice, corn, and other field and row crops (Dybala et al., 2017). To characterize the temporal and annual variation in habitat availability and energy supply across all of these land cover types, we first compiled data on the extent of open water in the Central Valley by land cover type and date for each water year (Point Blue, 2019; Reiter, Elliott, et al., 2015; Reiter et al., 2018). Briefly, these data are derived from supervised classification of satellite imagery of the Central Valley from Landsat 8 Operational Land Imager and Thermal Infrared Sensor, on ~ 16 -day intervals, with additional boosted regression tree models (Elith & Leathwick, 2009) used to estimate the probability of open water for pixels masked by cloud cover. Predictors included previous probability of open

water, proportion of land covers with open water in the surrounding area, the amount of flooding in the MODIS (Moderate Resolution Imaging Spectroradiometer) 8-day composite determined from the normalized difference water index (NDWI), recent precipitation in the region, and current and previous water year type as defined by the California Department of Water Resources (see Reiter et al., 2018 for details). These maps of open water were then summarized across the Central Valley as the proportion of several major land cover types with open water for that date.

Following Reiter et al. (2018), we corrected these estimates of the proportion of land covers with open water for small differences found between ground-truthed data and the remotely sensed data for each land cover type. These included an average of 11% of managed wetlands pixels incorrectly classified as not having open water when they did, and an average of 5% of corn pixels and 4% of rice pixels incorrectly classified as having open water when they did not. We further corrected these proportions to separate the contributions of rice fields enrolled in incentive programs from those flooded post-harvest without incentives. We assumed any rice fields enrolled in incentive programs on the date of each satellite imagery would be counted in the total number of rice pixels estimated to have open water on that date. Therefore, we subtracted the number of pixels corresponding to the total area enrolled in incentive programs from the estimated total number of rice pixels with open water on that date. Thus, the remaining proportion of rice pixels with open water represented the proportion of rice with open water that was not enrolled in an incentive program.

For wetlands, corn, and rice not enrolled in incentive programs, we then modeled the proportion of each land cover type that had open water as a function of day of year (where day 1 = 1 July) in each non-breeding season. Following Dybala et al. (2017) and Reiter et al. (2018), we fit separate generalized additive mixed models for each land cover type (Wood, 2006; Wood & Scheipl, 2020), allowing the shape of the function to vary among the four non-breeding seasons to account for variation in the open water curve. Models used a binomial error distribution and included random intercepts for each observation date to account for over-dispersion (Browne et al., 2005). To further minimize uncertainty in the estimates of the proportion of land covers with open water, we excluded any estimates derived from satellite imagery with <75% coverage of the cover type after cloud-filling. We also weighted each remaining data point by the proportion of original cloud-free cells observed in each satellite image, so that we relied less on estimates derived from images with more cloud cover. We used these

models to predict the daily proportion of each land cover type with open water between 1 July and 15 May for each of the four non-breeding seasons of the study.

To convert the daily proportion of landcovers with open water to an areal extent of available habitat in each land cover type, we combined these predicted values with estimates of the total areal extent of each land cover type in the Central Valley. We used a single estimate for each land cover type for all years included in this study, based on the 2015 estimated extent of managed wetlands and the 2007–2014 estimated average extents of rice and corn (excluding corn grown in the San Joaquin Valley, which is rarely flooded postharvest; Dybala et al., 2017). The effects of annual variation in the actual acreage of rice and corn planted during each year of the study on the extent of available habitat for shorebirds in each crop type was already represented in the annual variation in the open water curve described above. Because the satellite-derived estimates of the proportion of each crop class with open water were based on a sample of pixels that were consistently assigned to each crop class over the period 2007–2014 (Reiter et al., 2018), and were not updated annually, recently fallowed rice or corn were still incorporated into the estimated proportion with open water of each crop type. Therefore, a reduction in the estimated proportion with open water across years may represent either a reduction in the practice of post-harvest flooding that year, or a reduction in the total area planted, or both.

We used a different approach to estimate the contributions of the “other row and field crops” land cover type to the total habitat available for shorebirds. The total areal extent of this crop class has declined substantially in recent years compared to the 2007–2014 average (NASS, 2019), such that the summaries derived from Water Tracker may include a considerable proportion of different crop types (e.g., orchards) that have recently replaced it. Also, because the proportion with open water for “other row and field crops” was previously estimated to reach a peak of only 0.03 in the previous study, this land cover type contributed little to the seasonal variation in habitat availability and energy supply relative to wetlands, rice, and corn (Dybala et al., 2017). Consequently, across all water years in this study, we represented the average amount of additional habitat provided by this land cover type using the current average areal extent planted, 2013–2016 (NASS, 2019) combined with the previously developed open water curve for this crop class from the years 2007–2014 (Dybala et al., 2017).

Finally, because many shorebird species do not forage in water >10 cm deep (Elphick & Oring, 1998; Isola et al., 2000; Safran et al., 1997), it was also necessary to correct for the proportion of the open water habitat that

is shallow and accessible to most foraging shorebirds. For each of the land cover types, including separate estimates for seasonal and semi-permanent wetlands, we adopted previously established estimates for the daily average proportion of open water that was of suitable depth for foraging by most shorebirds (Dybala et al., 2017). We assumed these estimates did not vary substantially among years and thus used the same values for all years. By combining the daily estimates of the areal extent of open water habitat available to shorebirds with the daily estimates of the proportion that is shallow, we derived daily estimates of the areal extent of accessible habitat.

Contributions of incentive programs

To characterize the additional contribution of incentive programs to annual shorebird habitat and food energy supply we used an approach like that described above for the non-incentivized habitat. For each of the four non-breeding seasons, we compiled data on the total extent of rice fields enrolled in BirdReturns and the specific flood dates for each field (Dybala & Golet, 2022). To estimate the daily proportion of all enrolled fields that had open water, we assumed program requirements were followed. For the BirdReturns program, we assumed open water was maintained on 100% of the area of enrolled fields throughout the entirety of their individual enrollment period. For the WHEP Variable Drawdown practice, we assumed a staggered flood-up over November and December, which varied slightly between years based on general water availability and program requirement adherence. Specifically, in 2013–2014 we specified 50% flood-up on 1 November and 50% on 1 December; in 2014–2015 we specified 50% flood-up on 1 December and 50% on 15 December; in both 2015–2016 and 2016–2017 we specified 50% flood-up on 1 November and 50% on 15 November. Following flood-up, we assumed 100% of enrolled fields maintained open water through 1 February, and that drawdown was staggered in February, such that drawdown was initiated on 25% of the acres enrolled during each week of the month (Sesser et al., 2018). For the WHEP Fall Flooding practice, we assumed 100% of enrolled fields maintained open water for the required 14 days. However, because we only had data on the total acres enrolled in this program, and not the exact timing of each field's flooding, we assumed the availability of these acres was evenly distributed throughout the program period from 1 July through 15 September. In addition, for all of these incentive programs, we assumed fields continued to have open water for an average of 2 weeks following the end of their programs during which time the water gradually drained, percolated into the soil, or evaporated. This assumption was

consistent with expectations for the WHEP Fall Flooding practice and previous observations of the WHEP Variable Drawdown program (MBCP 2014; Sesser et al., 2018).

We summed the area of all fields enrolled in each incentive program on each day of each non-breeding season (1 July–15 May), including through the 2 weeks of gradual drawdown, to estimate the total area of open water identified in Water Tracker imagery (described in the previous section) that should be assigned to the incentive programs rather than the background amount of non-incentivized open water. Therefore, if compliance with the incentive programs in maintaining open water during these programs was <100%, or the drawdown period following incentive program enrollment periods was <2 weeks, we would have overestimated the contributions of the incentive programs and underestimated the background amount of open water habitat available. This may be particularly likely in fall, when high temperatures contribute to high rates of evaporation. On the other hand, we may have underestimated carry-over effects of the incentive programs beyond the 2 weeks of gradual drawdown, particularly in spring when fields that already had saturated soil were more likely to pond and passively create additional open water habitat following precipitation (Golet et al., 2018). Therefore, particularly during the wet springs of 2016 and 2017, our estimate of the contribution of these incentive programs to the availability of open water habitat may be conservative.

To account for the proportion of the incentivized open water habitat that was shallow and accessible to foraging shorebirds in the BirdReturns program, we estimated of the proportion accessible based on monitoring data from depth stakes and estimates of compliance with the program's rules to maintain depths <10 cm (Dybala & Golet, 2022). For fall BirdReturns enrollments (15 August–28 October), these included estimates of 70% compliance until 1 October (30% too deep), rising to 80% compliance by 14 October, and then 90% compliance by 1 November and through the remainder of the program. For spring enrollments (1 February–14 April), these included similar estimates of 70% compliance on 1 February, rising to 80% by 15 February, 90% by 22 February, and 100% by 1 March. For both seasons, we used natural splines to generate daily estimates of the proportion accessible that smoothly transitioned between observations on these dates.

For the WHEP Fall Flooding practice, we lacked comparable information about compliance with the program's guidelines to maintain depths <10 cm. We thus used our professional judgment based on anecdotal observations made during bird monitoring to assume 90% compliance, while recognizing considerable uncertainty.

However, due to the relatively small number of acres involved, we expect that this assumption had little effect on the results. For the WHEP Variable Drawdown practice, we applied the previously established estimates developed for rice fields, which were developed in part from data collected on fields enrolled in the WHEP Variable Drawdown practice (Dybala et al., 2017). We again assumed these estimates of daily proportion accessible did not vary substantially among years and combined them with the daily areal extent of incentivized available habitat to estimate the daily extent of incentivized accessible habitat.

Energy supply and demand

We assumed the daily energy needs of the shorebird community varied throughout the non-breeding season as the total abundance and composition of the community changes, and due to increased energy needs in preparation for spring migration (Dybala et al., 2017). For the energy content of benthic invertebrates accessible to shorebirds in open water of suitable depth, we used previous estimates for managed wetlands of 186.6 MJ ha^{-1} (95% CI: 97.9–355.5), and for rice of 104.9 MJ ha^{-1} (66.6–165.4; Dybala et al., 2017). We assumed this energy content was not different for rice fields enrolled in incentive programs, and due to a lack of comparable data in flooded agricultural fields other than rice, we followed Dybala et al. (2017) in applying estimates from rice to corn and other crops. Any newly added open water habitat was assumed to start with the total energy density for the land cover type. Also following Dybala et al. (2017), we did not account for consumption of invertebrates by other predators such as ducks, or any differences in invertebrate food resources that may have resulted from differences in the timing or duration that individual fields were flooded. Not doing so likely introduced some bias in estimates of food energy available to shorebirds; however, the magnitude and direction of these effects was not sufficiently well established to merit their inclusion in the model. Applying these assumptions, we followed the approach described by Dybala et al. (2017) to calculate the net change in open water habitat available between daily time steps, where a net increase represents the minimum amount that was just added and a net decrease represents the minimum amount of previously existing habitat that went dry. The starting energy content in any newly added open water was gradually depleted each day as proportions of this total energy density became accessible to foraging shorebirds, and proportions of the accessible energy supply were consumed. At the end of each daily time step, any remaining unconsumed energy

supply was assumed to redistribute evenly across the total area of open water in each land cover type and carry over to the following day, minus any energy supply lost in areas that went dry. Consumption of food energy by foraging shorebirds was assumed to be proportionally distributed across land cover types according to the daily energy supply available (ideal free distribution, Fretwell and Lucas 1969), and periods of shortfall were identified when model outputs indicated that all of the food in the fields was consumed.

We compared daily food energy available to daily shorebird energy needs for both an assumed Central Valley baseline non-breeding shorebird population size and a long-term population size objective established by the Central Valley Joint Venture (CVJV, 2020). Dybala et al. (2017) derived the baseline estimate from surveys conducted throughout the Central Valley from 1992 to 1995 by Shuford et al. (1998). Although it is not known whether the non-breeding shorebird population size in the Central Valley has changed since these baseline surveys were conducted, these estimates serve as a useful benchmark for setting both short- and long-term conservation objectives. In recognition of the huge losses of wetland habitat that occurred prior to the 1990s (Frayer et al., 1989), the CVJV defined the long-term population size objective as a doubling of the Shuford et al. (1998) baseline and established an associated long-term conservation objective of increasing the amount of habitat to a level that would support this increased population size (CVJV, 2020).

Model fitting

Using the data described above to parameterize the previously developed bioenergetics model, we evaluated the timing and magnitude of shortfalls in energy supply to shorebirds during the four non-breeding seasons of the study. Energy shortfalls occur whenever the daily energy need exceeds the daily energy supply, indicating when additional habitat is required to support the non-breeding shorebird community. We examined energy shortfalls under four scenarios. These included combinations of two levels of population size (baseline and doubling of the baseline [CVJV objectives]), and habitat availability (with and without the contribution of habitat incentive programs). We assumed that fields enrolled in the incentive programs would not have been flooded during the enrollment periods if these programs had not existed, and thus would not have contributed to the energy supply available to shorebirds. This assumption may have been violated for some fields, causing our estimates of the contribution of incentive programs to be biased high,

however, we expect that this effect was small. This is because most of our study took place during drought conditions when winter flooding of rice fields was reduced in the Sacramento Valley (Reiter et al., 2018), and because the incentive programs prioritized early and late season habitat outside of the time periods when rice fields are conventionally winter flooded.

For the scenarios that excluded any habitat from incentive programs, we then estimated the timing and minimum extent of additional habitat that would have been required to eliminate all energy shortfalls, for both the baseline and the doubling population sizes. To accomplish this, we iteratively added 50-ha blocks of habitat in a schedule similar to the BirdReturns program, with a duration of 1 month and staggered by half-months (e.g., intervals of 1–31 July, 16 July–15 August, etc.), until no shortfalls remained. For simplicity, we assumed that these additional blocks of habitat were managed for depth to remain 100% accessible to shorebirds, and that they contained the same energy density as rice fields.

Finally, using Monte Carlo simulation, we examined the uncertainty in our estimates of the total accessible open water habitat available to shorebirds, the energy content in that habitat, and the resulting magnitude of the energy shortfalls for each scenario and year. Following Dybala et al. (2017), for each of 1000 iterations of the bioenergetics model for each scenario and year, we generated random values of the energy content for each land cover type, drawn from a log-normal distribution with observed mean and standard deviation. We also generated random values for the model parameters that predicted the daily proportion of each land cover with open water. For the proportion of open water that is of suitable depth, we used the original resamples used in the prior analysis (Dybala et al., 2017). This included resamples of the original model parameters predicting the daily proportion accessible in rice, and because this model was originally derived from data that included WHEP Variable Drawdown fields, we applied these error estimates to both non-incentivized rice and WHEP Variable Drawdown fields. The original resamples also included the addition of error to the estimated daily proportion accessible in managed seasonal and semipermanent or permanent wetlands derived from expert opinion; error estimates were drawn from a logistic distribution with a location of 0 and a scale of 0.25. We extended this same approach to incorporate uncertainty in the daily proportion accessible for fields enrolled in BirdReturns and WHEP Fall Flooding programs. Using the 1000 samples of each parameter, we used the 2.5th and 97.5th percentiles to estimate the 95% confidence intervals in the amount of accessible open water habitat available to shorebirds, as well as the total magnitude of the energy shortfalls resulting from each iteration of the bioenergetics model.

We fit all models in R version 4.1.0 (R Core Team, 2021) using the custom package *bioenermod* v. 0.1.0 (Dybala, 2016).

RESULTS

Annual and temporal availability of non-incentivized habitat

Across the four non-breeding seasons of our study and in comparison with previous estimates, we found some evidence for variation in the timing and extent of non-incentivized flooding in the Central Valley, primarily in rice (Figure 1). While the timing of fall flood-up and

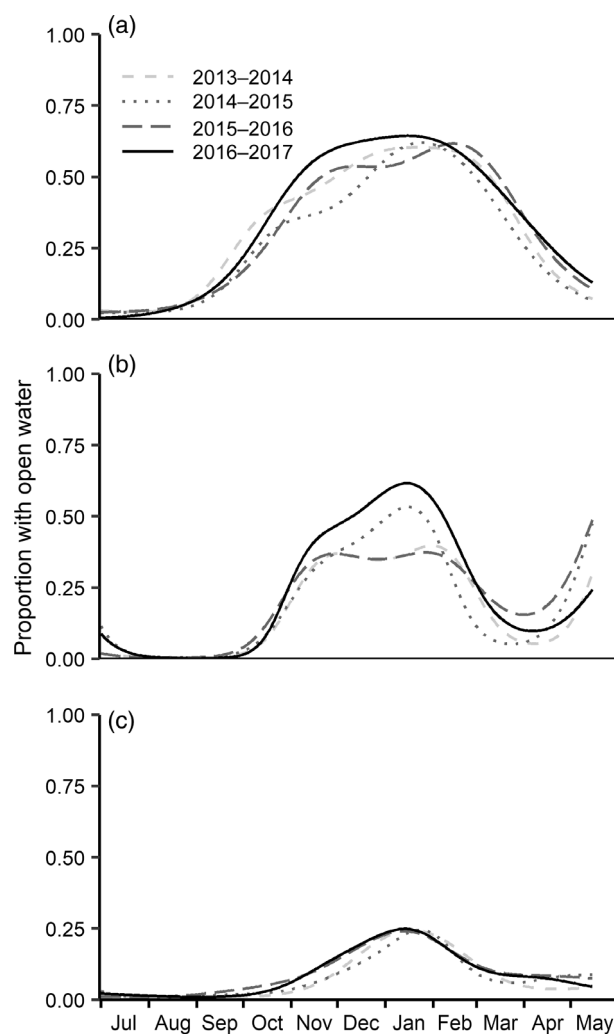


FIGURE 1 Annual and seasonal variation in the model-predicted proportion of three main waterbird habitat types with open water in the Central Valley: (a) managed wetlands, (b) rice, and (c) corn. Estimates for other field and row crops were taken from (Dybala et al., 2017; see *Methods*). For clarity, confidence intervals are not shown.

spring draw-down was fairly consistent across years, the peak proportion of rice with open water appeared to be truncated in 2013–2014 and 2015–2016, reaching only 0.40 (95% CI: 0.29–0.51) and 0.37 (0.28–0.48), respectively, compared to 0.62 (0.51–0.72) in 2016–17 and the previously estimated average of 0.69 (0.48–0.84) over the period 2007–2011 (Dybala et al., 2017). In managed wetlands and corn, the proportion of the land cover with open water was more consistent across the four years, with peak estimates for managed wetlands ranging from 0.60 (0.56–0.65) in 2013–2014 to 0.64 (0.61–0.68) in 2016–2017, and peak estimates in corn ranging from 0.24 (0.20–0.30) in 2013–2014 to 0.25 (0.20–0.31) in 2016–2017. While the peak estimates in corn were similar to the previously estimated average of 0.22 (0.15–0.30) over the period 2007–2011, we noted that the peak estimates in wetlands were all lower than the previous average of 0.81 (0.76–0.86; Dybala et al., 2017). Similarly, the estimated proportion of managed wetlands with open water during July–August (daily point estimates ranging 0.01–0.08) and April (ranging 0.07–0.35) were also lower than previous estimates (ranging 0.09–0.12 and 0.27–0.48, respectively; Dybala et al., 2017).

This annual variation in the extent of non-incentivized flooding resulted in variation in the timing and extent of total open water and accessible open water habitat available to foraging shorebirds (Figure 2), and therefore, variation in the estimated timing and magnitude of energy shortfalls (Figure 3). Excluding the contributions of incentive programs, we estimated that the total number of ha-days of accessible open water habitat over each non-breeding season would have increased over the four years of the study such that totals were lowest in the critically dry years of 2013–2014 and 2014–2015 and highest in the wet year of 2016–2017 (Table 3). For both population size scenarios, we estimated that there would have been energy shortfalls in each year of the study, with the highest cumulative total energy shortfall in the critically dry year of 2013–2014, although the 95% confidence intervals for each year overlapped considerably (Table 3 and Figure 3).

Contributions of incentive programs

Incentive programs contributed additional habitat in each year of the study (Table 2). In terms of total area enrolled, the largest program in each year was WHEP Variable Drawdown, although there was a declining trend in enrollments over the study period. The smallest program in each year was WHEP Fall Flooding. The BirdReturns program did not incentivize any habitat in the fall of the first non-breeding season of this study

(2013), but in subsequent years it more evenly divided investment in the fall and spring enrollment periods. Combined, the total area enrolled in incentive programs was highest in the first two years of the study and fell to less than half of that in 2016–2017, when some spring contracts in BirdReturns were canceled due to wet weather. In terms of accessible open water habitat, the largest contribution from incentive programs was in 2013–2014, with an addition of ~14% over the relatively low amount of accessible open water habitat otherwise available that year, and the smallest contribution was in 2016–2017, with an addition of ~4% to the relatively large amount already available that year (Table 3). Thus, the incentive programs reduced both annual variation in the amount of accessible open water, and shorebird energy shortfalls in all four years. Although confidence intervals overlapped considerably, we estimated that incentive programs had the largest impact in 2013–2014, the year with the largest total enrollment, reducing energy shortfalls by 22% for the baseline population scenario and 15% for the doubling scenario (Table 4).

Annual and temporal variation in habitat needs

For both the baseline and the doubling population scenarios, across all four years of study, we identified a consistent pattern of energy shortfalls, regardless of whether or not the habitat contribution of incentive programs was included. Shortfalls occurred during two distinct periods: early and late in the non-breeding season (hereafter, “fall” and “spring,” respectively; Figures 3 and 4). We also found that energy shortfalls were more consistent in magnitude and timing during the fall than the spring. No energy shortfalls were identified from October through early January in any year under either population scenario (Figure 5).

For the baseline population scenario, and excluding the contribution of incentive programs, lower confidence limits for the fall energy shortfall were consistently greater than zero from late July to late August, reflecting high confidence that an energy shortfall occurred during this period in all four years (Table 4; Figures 3 and 5). In addition, mean energy shortfall estimates were consistently greater than zero from mid-July through the end of August, when little open water habitat was accessible outside of managed wetlands. In some years, shortfalls were greater than zero as early as 1 July and as late as mid-September.

For the doubling population scenario, the fall shortfall period was larger in magnitude and extended over a longer period than in the baseline scenario. There was

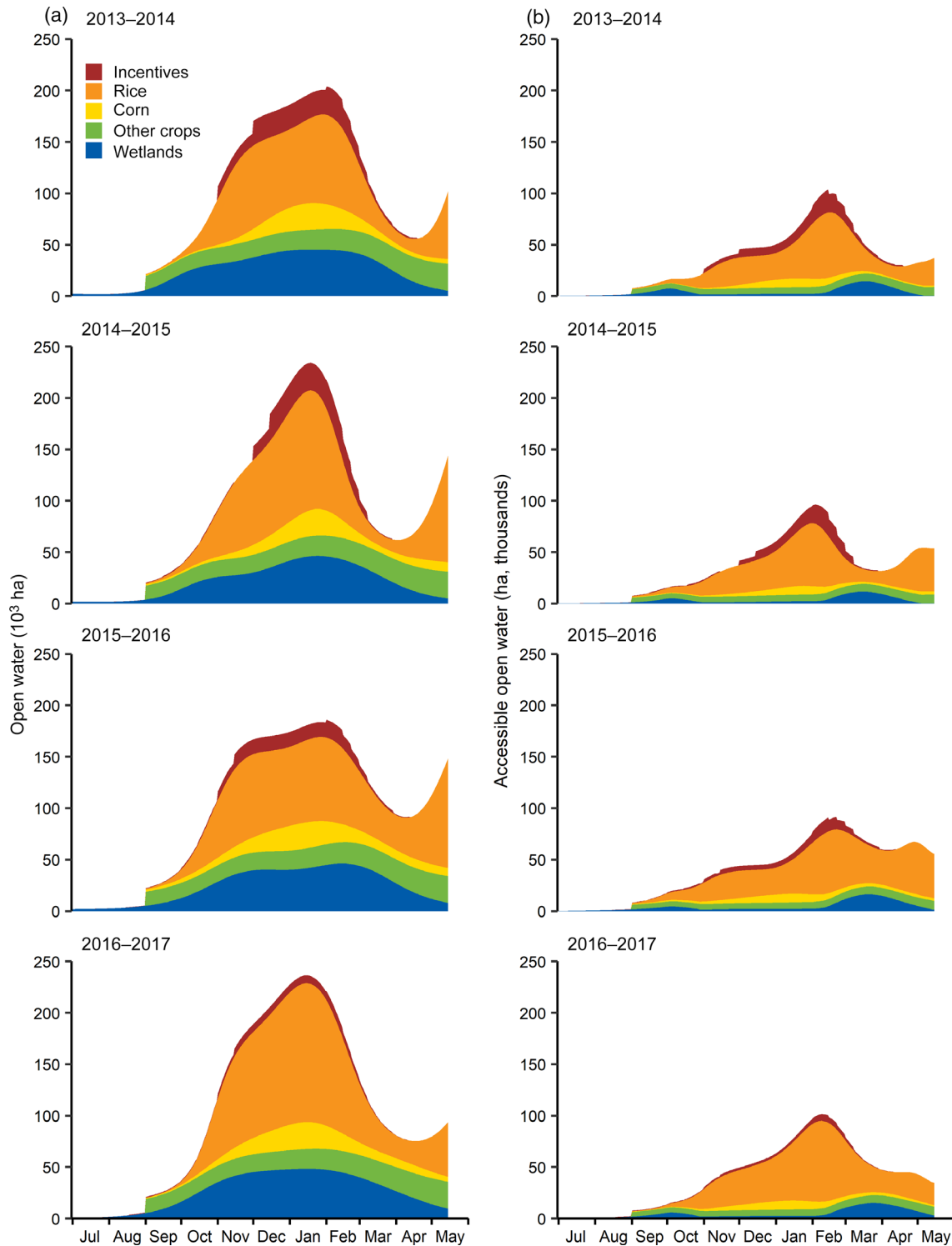


FIGURE 2 Annual and seasonal variation in the estimated (a) total open water habitat and (b) accessible open water habitat available to foraging shorebirds, including the contribution of incentive programs.

high confidence in a consistent energy shortfall extending from mid-July through the end of August, with mean shortfalls greater than zero consistently observed from early July through mid-September (Figures 3 and 5). In the most extreme cases under this scenario mean energy

shortfalls above zero extended from 1 July through the end of September.

The timing of the WHEP Fall Flooding program (1 July through 15 September) overlapped well with the timing of these fall energy shortfalls, but enrollment was

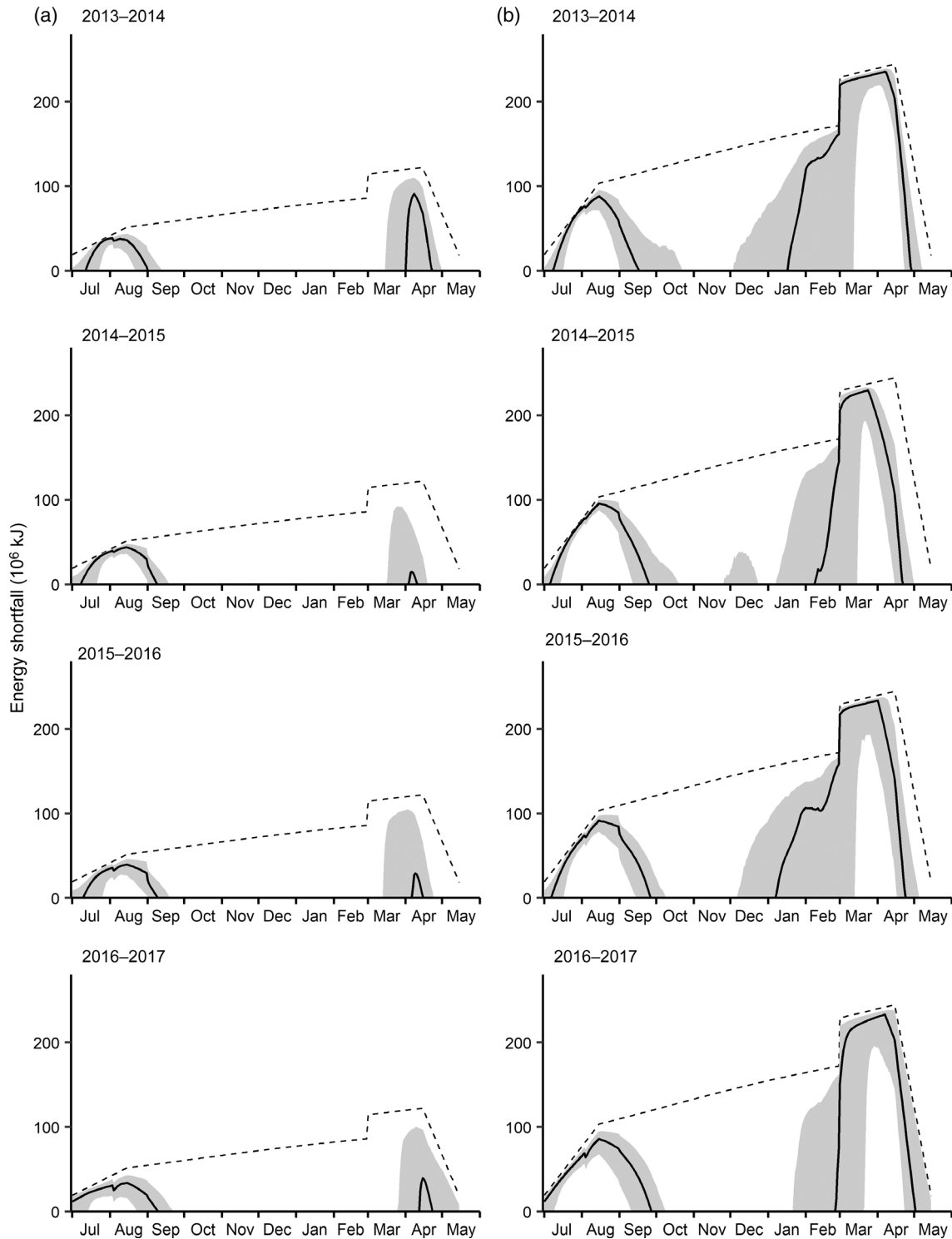


FIGURE 3 Annual and seasonal variation in the estimated timing and magnitude of energy shortfalls, excluding the contributions of any incentive programs, for (a) the baseline population scenario and (b) the population objectives scenario. The solid black lines indicate the mean shortfalls, and the gray bands are the 95% confidence intervals from Monte Carlo simulation. The daily energy requirements for the entire shorebird community are shown as dashed lines (from Dybala et al., 2017).

relatively small during the four years of this study (Table 2). Fall enrollments in the BirdReturns program were larger but did not start until 15 August at the earliest. Consequently, the estimated impact of incentive

programs at reducing fall energy shortfalls was relatively small, ranging -0.8% to -5.7% for the baseline population scenario and -0.3% to -2.7% for the doubling scenario (Table 4). Model results indicate only brief periods

TABLE 3 Estimated total millions of ha-days of accessible open water habitat for foraging shorebirds by land cover type and incentive program, shown with 95% confidence intervals estimated from Monte Carlo simulation.

Habitat/program	2013–2014		2014–2015		2015–2016		2016–2017	
Non-incentivized habitat								
Wetlands	1.30	(0.78–2.11)	1.04	(0.63–1.73)	1.340	(0.88–2.17)	1.48	(0.93–2.31)
Rice	6.15	(3.19–9.70)	6.60	(3.14–10.71)	7.91	(4.40–12.01)	8.26	(4.18–13.11)
Corn	0.84	(0.22–1.94)	0.85	(0.22–1.94)	1.04	(0.27–2.42)	0.99	(0.26–2.29)
Other crops	1.68	(0.39–3.62)	1.63	(0.39–3.62)	1.63	(0.39–3.62)	1.63	(0.39–3.62)
Total non-incentivized	9.92	(6.36–13.98)	10.12	(6.35–14.93)	11.97	(8.22–16.77)	12.4	(7.93–17.86)
Incentivized habitat								
BirdReturns fall	0.00	(0.00–0.00)	0.058	(0.044–0.065)	0.062	(0.048–0.071)	0.043	(0.032–0.050)
BirdReturns spring	0.23	(0.21–0.24)	0.068	(0.061–0.072)	0.15	(0.14–0.16)	0.062	(0.056–0.065)
WHEP Fall Flooding	0.004	(0.003–0.004)	0.004	(0.003–0.004)	0.001	(0.000–0.001)	0.004	(0.004–0.004)
WHEP Variable Drawdown	1.16	(0.49–1.91)	1.09	(0.489–1.71)	0.73	(0.31–1.22)	0.39	(0.16–0.65)
Total incentivized	1.39	(0.72–2.14)	1.22	(0.62–1.83)	0.94	(0.52–1.43)	0.50	(0.27–0.75)
Grand total	11.30	(7.21–16.05)	11.34	(7.03–16.69)	12.92	(8.77–18.05)	12.85	(8.21–18.60)

TABLE 4 Total cumulative food energy shortfalls (kJ, billions), and estimated differences (%) when incentive programs are included or excluded, by year and season, for the baseline population and the population objectives scenarios.

Time period	Baseline population			Population objectives						
	Excluding incentive programs	Including incentive programs	Difference (%)	Excluding incentive programs	Including incentive programs	Difference (%)				
Fall										
2013	1.42	(0.86–1.98)	1.40	(0.85–1.97)	–0.8	3.90	(2.77–6.46)	3.88	(2.76–5.71)	–0.3
2014	1.91	(1.33–2.37)	1.84	(1.31–2.27)	–3.9	4.91	(3.80–6.65)	4.78	(3.73–6.01)	–2.7
2015	1.69	(1.01–2.18)	1.63	(0.97–2.12)	–3.4	4.78	(3.53–6.90)	4.68	(3.45–5.78)	–2.1
2016	1.67	(0.95–2.33)	1.57	(0.92–2.21)	–5.7	4.78	(3.24–6.04)	4.67	(3.14–5.90)	–2.4
Spring										
2014	1.31	(0.00–3.50)	0.72	(0.00–2.30)	–45.0	16.53	(8.29–19.66)	13.56	(6.48–17.71)	–18.0
2015	0.07	(0.00–2.00)	0.00	(0.00–1.31)	–100.0	10.71	(4.70–16.06)	8.58	(3.67–13.37)	–19.9
2016	0.17	(0.00–2.78)	0.00	(0.00–1.81)	–100.0	15.25	(6.08–18.61)	13.29	(4.84–17.60)	–12.8
2017	0.27	(0.00–2.55)	0.12	(0.00–2.26)	–56.1	11.76	(5.63–17.56)	11.07	(5.25–16.52)	–5.9
Total										
2013–2014	2.72	(0.95–5.11)	2.12	(0.88–3.98)	–22.0	20.43	(11.62–25.49)	17.44	(9.60–22.71)	–14.6
2014–2015	1.98	(1.34–4.16)	1.84	(1.31–3.38)	–7.1	15.63	(8.87–22.23)	13.36	(7.89–18.90)	–14.5
2015–2016	1.86	(1.03–4.74)	1.63	(0.98–3.63)	–12.2	20.03	(10.20–24.98)	17.98	(8.82–23.15)	–10.3
2016–2017	1.94	(0.96–4.64)	1.69	(0.92–4.24)	–12.7	16.54	(9.48–22.88)	15.74	(9.07–21.82)	–4.9

Note: Energy shortfalls are shown with 95% confidence intervals estimated from Monte Carlo simulation. Negative values in % difference represent reductions in shortfalls.

of time when the incentive programs reduced the fall energy shortfalls (Figure 4), corresponding with the initial flood-up of new fields in each program. In all four years, the incentive programs were insufficient to substantially reduce the estimated fall energy shortfalls for shorebirds in the Central Valley.

Spring energy shortfalls were more variable in magnitude and timing than fall shortfalls. In addition, they had more uncertainty in their estimates, at least in part because they depended on habitat availability and energy consumption during all prior time steps. For the baseline population scenario, mean energy shortfalls were

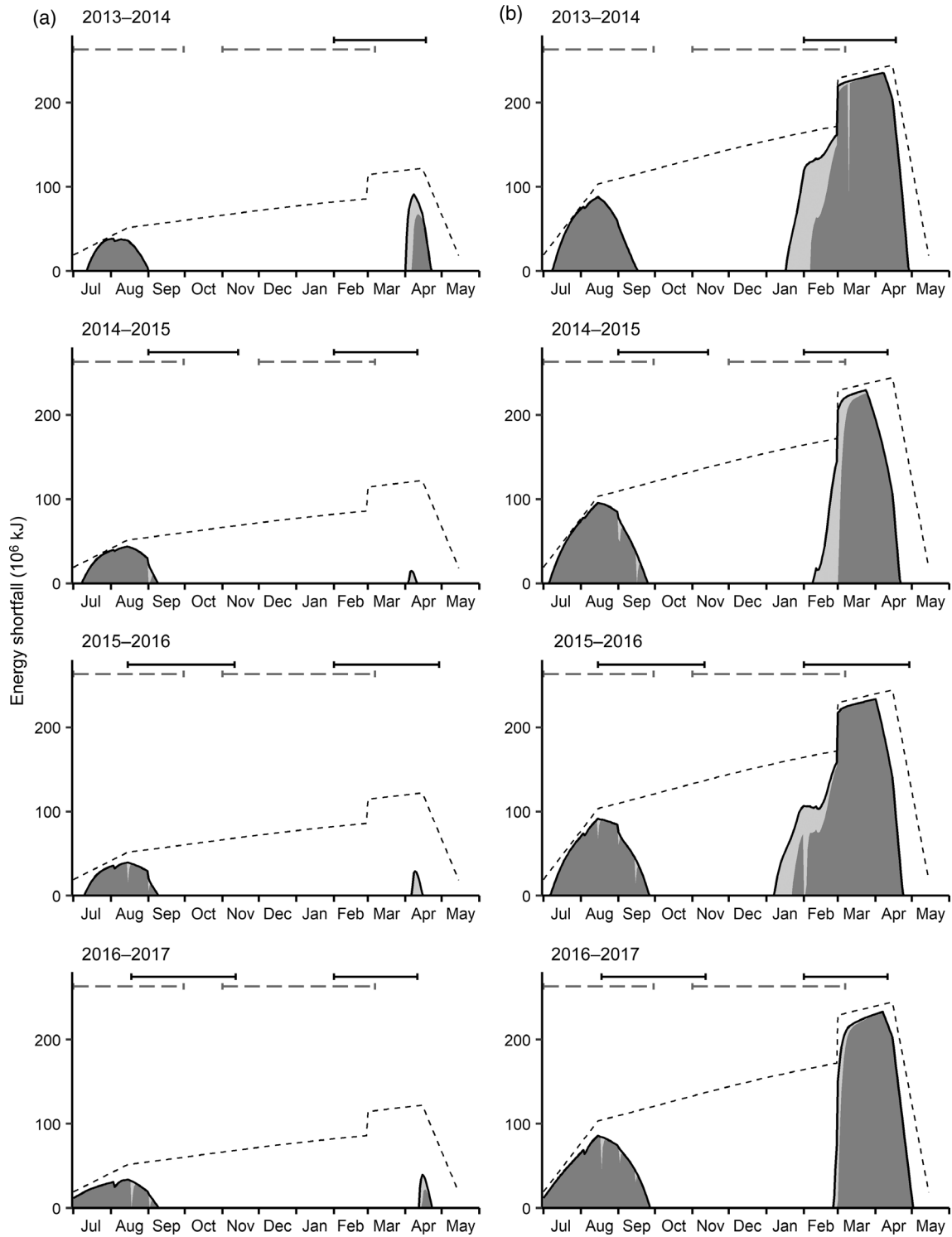


FIGURE 4 Annual and seasonal variation in the estimated timing and magnitude of energy shortfalls for (a) the baseline population scenario, and (b) the population objectives scenario. The dark gray area corresponds to the energy shortfalls when incentive programs are included, while the light gray area shows the additional energy shortfalls incurred when incentive programs are excluded. The black lines identify the mean energy shortfalls with incentive programs excluded. There were no fall incentive programs in 2013. Also shown are the daily energy requirements of the entire shorebird community (dashed lines; from Dybala et al., 2017), and the annual and seasonal timing of BirdReturns (solid black horizontal bars) and the Waterbird Habitat Enhancement Program (WHEP; dashed gray horizontal bars) incentive programs.

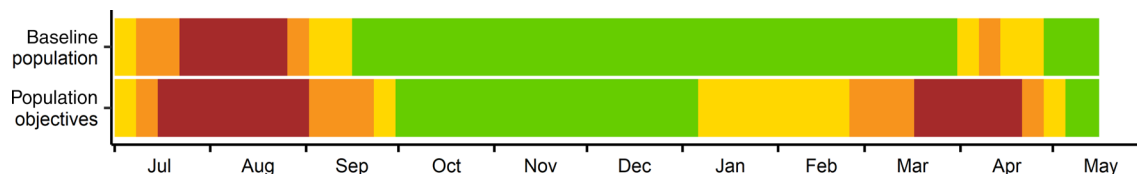


FIGURE 5 Consistency and confidence in the timing of Central Valley shorebird habitat shortfalls for the baseline population scenario and the population objectives scenario, excluding the contributions of any incentive programs. Shown here are weeks with, (1) in red, lower confidence limits for the energy shortfall estimate that are consistently greater than zero in every year of this study; (2) in orange, mean energy shortfalls that are consistently greater than zero in every year of this study; (3) in yellow, mean energy shortfalls greater than zero in some (1–3) years only; or (4) in green, mean energy shortfalls never greater than zero in any year.

consistently greater than zero in mid-April, and sometimes greater than zero throughout the entire month, although the lower confidence limit for these estimates never exceeded zero (Table 4 and Figure 3). For the doubling scenario, the larger size of the shorebird community more rapidly consumed the available food supply through the winter, resulting in spring energy shortfalls that began earlier and were substantially larger (Figure 3). Excluding the contributions of the incentive programs, lower confidence limits were consistently greater than zero across all four years from mid-March through late April, with mean energy shortfalls consistently greater than zero from late February through the end of April (Figure 3). In some years, mean energy shortfalls were greater than zero as soon as early January and persisted as late as early May.

The timing of spring enrollments in the BirdReturns program (1 February–14 April) overlapped with the timing of the most consistent spring energy shortfalls (March–April), while the timing of the WHEP Variable Drawdown program, which primarily created accessible habitat in February, overlapped with the earlier timing of energy shortfalls that result under the doubling population scenario, particularly during the first three drier years (Figure 4). Because of this alignment in time and the large enrollment in the WHEP Variable Drawdown program, the estimated impact of the incentive programs on mean spring energy shortfalls were larger than in the fall, with reductions ranging from 45.0% to 100.0% for the baseline population scenario and 5.9% to 19.9% for the doubling scenario. We also found that the habitat incentive programs delayed the onset of shortfalls, especially in spring, under the doubling scenario, during the drier years (Figure 4).

To eliminate the mean energy shortfalls for the baseline population scenario through implementation of incentive programs similar to BirdReturns, we estimate that a minimum fall enrollment of 14,000 ha staggered between 1 July and 31 August would have been required in each year, but up to 18,000 ha and extending to 15 September in some years (Figure 6; Appendix S1). A

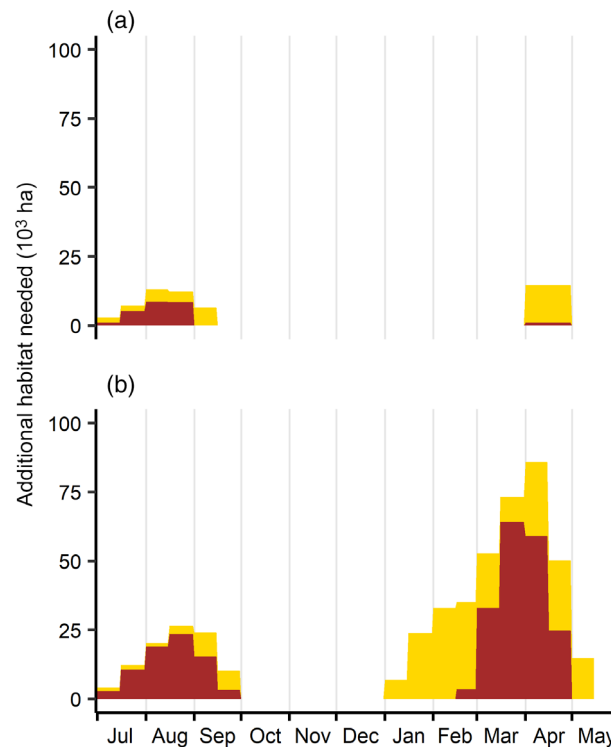


FIGURE 6 Estimated range of total incentive habitat required to eliminate energy shortfalls for (a) the baseline population scenario and (b) the population objectives scenario. We assumed programs would incentivize the flooding of additional rice fields for 1 month in duration, staggered by a half-month. The filled red area represents the minimum amount of incentivized habitat required during each half-month across all four years of the study, and yellow represents the maximum amount. See Appendix S1 for annual details.

minimum of 1050 ha enrolled would also be required during April, but up to 14,550 ha in some years. For the doubling scenario, fall enrollments should extend through 30 September and increase to 37,800–47,450 ha. For the spring shortfalls, which vary considerably in both magnitude and timing, we estimated a minimum of 105,950 ha of habitat would have been required staggered

between 1 February and 30 April and up to 171,700 ha in some years ranging from as early as 1 January to as late as 15 May.

DISCUSSION

Worldwide, as natural habitats continue to be lost and greater demands are placed on land and water, actively managed areas are becoming increasingly important for meeting the habitat needs of migratory species (Stralberg et al., 2011; Whittingham, 2011). Yet often the projects that are implemented to meet these needs are hampered by a lack of information on when, where, and how much habitat is needed at different points in time (Evans & Green, 2007), and how this can change under differing environmental conditions (Moilanen et al., 2014). Understanding these issues is especially important in highly dynamic systems such as wetlands where habitat conditions can vary greatly both within and among years. Already-observed shifts in habitat conditions resulting from climate change amplify the importance of quantifying habitat needs (Sutherland et al., 2012), especially for species such as shorebirds that appear to migrate in response to endogenous cues, as opposed to climatic signals (Both and Visser 2001; Lehikoinen et al., 2004). In this study, we addressed these issues for migrating and overwintering shorebirds in California's Central Valley by conducting bioenergetic analyses to identify and characterize habitat shortfalls over four successive years that differed greatly in environmental conditions.

For the baseline population scenario, we found a high level of consistency in the timing and magnitude of habitat shortfalls over these four years, despite large differences in annual rainfall. Incentive programs that were implemented to provide supplemental habitat were somewhat effective in reducing these shortfalls, but there were consistent unmet habitat needs during early fall migration (mid-July through August), when there was little accessible open water habitat available. The consistent need for more habitat in fall was present regardless of how much rain fell in the previous wet season. Some of the highest shorebird densities ever recorded in Central Valley agricultural fields have been observed in fields flooded in early fall (Golet et al., 2018), affirming the need for habitat at this time.

Spring shortfalls arose in some years, but they were less consistent and of shorter duration than fall shortfalls. In all years, we identified a possible energy shortfall during April for the baseline population scenario; however, in two of the four years the mean shortfall was zero. Contrary to our expectation, the estimated spring shortfall in 2016–2017 did not appear to be lower than

in previous years, even though it was a year of very high rainfall. This may be because, although more rain fell overall in this year, spring was drier than in the previous two years, as reflected in lower open water. Overall, the amount of open water in agriculture in April is consistently low and has limited variability among years compared to other months in late winter and spring (February–May; Schaffer-Smith et al., 2017). In winter, across the four years we studied, which included an extended period of severe drought, there was always enough habitat to meet the energy needs of the baseline population.

In comparison, for the CVJV population objectives scenario (defined as double the baseline population size), habitat shortfalls were considerably greater and of longer duration. Shortfalls during fall migration were consistent in timing and magnitude across years, but those occurring during spring varied greatly, and in some cases appeared as early as mid-winter. During fall migration the Central Valley is hot and dry, and suitable habitat is only found where there is intentional flooding. Spring migration, in contrast, occurs toward the end of the rainy season when the combination of rainfall and intentional flooding practices typically provide a significant amount of shallow water shorebird habitat (Schaffer-Smith et al., 2017). This happens even following dry winters (this study), although to a lesser extent in the southern compared to northern Central Valley (Reiter et al., 2018). Insufficient spring habitat is a concern, however, toward the end of the migration period and in meeting the doubling goal, especially as increased temperatures associated with climate change exacerbate drying conditions (Diffenbaugh et al., 2015).

Comparison with previous shortfall estimates

Unexpectedly, the timing of fall energy shortfalls in this study shifted earlier and their duration increased relative to previous estimates developed based on average conditions from 2007 to 2014 (Dybala et al., 2017). We attribute this shift in the timing of energy shortfalls to reduced open water on wetlands during July–August in all four years of our study, which translated into reduced foraging habitat area. One factor that may explain this is the reduced duration of flooding during the severe drought of 2013–2015, which may have encouraged vegetation encroachment in wetlands (Byrd and Lorenz 2018) that persisted in subsequent years.

We also found that in spring non-breeding shorebirds may have become more food limited in recent years, particularly in April for the baseline population, and starting

as early as late February for the doubling scenario. As with fall, this may be partly attributed to the reduced proportion of managed wetlands with open water observed throughout the non-breeding season, as well as to a reduced peak proportion of rice with open water in some recent years. Surrounding these core habitat needs, our study identified a large time frame over which additional habitat may be needed, particularly in drier years, ranging from early January through early May. Our finding of reduced habitat availability for migratory shorebirds in the Central Valley in recent years is noteworthy because it is consistent with what was predicted to result from ongoing climatic warming (Barbaree et al., 2020; Matchett & Fleskes, 2017). From 1895 to 2017, the highest annual mean air temperatures ever recorded in California occurred in the last four years (coincident with our study), with 2014 being the warmest on record, followed by 2015, 2017, and 2016 (WRCC, 2018).

Effect of incentive programs

Previous analyses have demonstrated that Central Valley habitat incentive programs provide habitat to a broad suite of shorebirds and other waterbirds (Golet et al., 2018; Sesser et al., 2018; Strum et al., 2013). During the severe drought of 2013–2015, WHEP Variable Draw-down and BirdReturns at times provided over 60% of the available flooded habitat in the Central Valley (Reiter et al., 2018). Even so, our research suggests that these programs were insufficient to overcome the annual shortfalls that are typically present, even for the baseline population during and after wetter than average years. In fall of all four years, there were unmet needs, providing clear evidence that the scale of these programs needs to be increased, or additional habitat needs to be provided by other means.

For the baseline scenario, the spring habitat incentive programs had a much larger impact on reducing the energy shortfalls compared to the fall programs, such that in two of the years they were eliminated. Impacts of incentive programs were greater in spring because more habitat was created, the deficits that needed to be overcome were smaller, and the habitat was provided in advance of and during the shortfall, as opposed to mostly after, as with fall. Spring shortfalls modeled under the doubling scenario were much greater because most of the available food was consumed by the larger modeled population of birds before the programs began. Ideally incentive programs would be implemented before fall flooding of managed wetlands in September and October, which is too late for many shorebird migrants, as previously noted by Shuford et al. (1998). The bulk of fall incentive

program habitat was created during these same months, and hence was not optimally timed; however, habitat created at this time is still beneficial in that it delays depletion of food resources in spring, which is especially important under the doubling scenario.

Response of the birds to habitat shortfalls

Shorebird monitoring data collected during our study also suggest that there was insufficient habitat during early fall and late spring migration in the Central Valley, when shortfalls were documented for the baseline population scenario. During these times, birds crowded into areas that had accessible open water in incentive program post-harvest flooded rice fields, and measures of shorebird density and species richness were at their highest levels (Golet et al., 2018; Sesser et al., 2018). Recent telemetry work on shorebird movements in the Central Valley provides further information on how the birds responded to habitat limitations. This research documented Dunlin (*Calidris alpina*) and Long-billed Dowitchers (*Limnodromus scolopaceus*) moving from the Sacramento Valley as rice fields dried in spring to flooded wetlands being drawn down in the San Joaquin Valley, even though this is in the opposite direction of their migratory trajectory (Barbaree et al., 2018).

Future research needs

Our quantification of habitat shortfalls for shorebirds in the Central Valley could be improved by incorporating more spatial and temporal variation in the bioenergetics model, including variation in food energy content (Dybala et al., 2017) that is influenced by field management practices (Elphick et al., 2010). In addition, the model could be improved by better accounting for dynamic rates of energy consumption that vary temporally and spatially with local site-specific and landscape-scale factors (Albanese & Davis, 2013, 2015; Farmer & Parent 1997; Reiter, Wolder, et al., 2015), as well as with the presence of other taxa, such as waterfowl, which prey on invertebrates especially in spring (Drobney 1980). More recent population surveys would also be useful in that they would enable better characterization of temporal and spatial variation in the abundance and composition of the shorebird community. This would improve estimates of energy needs and help identify which species are benefitting most and least from current habitat programs and management practices. However, while this additional information would improve the precision of the timing and magnitude of our energy shortfall

estimates, it is unlikely to substantially change the results of our comparisons between wet and dry years, or our estimates of the contribution of incentive programs.

An additional critical question that should be addressed is whether fitness consequences are resulting from insufficient habitat and the associated food energy shortfalls that shorebirds appear to be experiencing in the Central Valley. To date, there is no direct evidence for this, yet studies from other regions suggest they may be likely (Piersma et al., 2016). Perhaps the most dramatic recent example comes from the Yellow Sea where loss of migratory habitat has been implicated in the decline of 10 species of shorebirds in the East Asian-Australasian Flyway (Studds et al., 2017). Other studies similarly emphasize the importance of high-quality migratory habitats that promote high rates of energy acquisition. Shorebirds with better nutritional status and body condition, have been shown to make fewer migratory stops and have higher apparent survival and future fecundity compared to poorer condition birds (Anderson et al., 2019, Swift et al., 2020). Even so, the response of shorebirds to habitat limitation is situation specific, and the extent to which Central Valley shorebirds may be able to have their needs met elsewhere (e.g., in San Francisco Bay or along the Pacific coast) remains to be determined.

Implications for future programs

The results of our analyses suggest concrete actions should be taken to advance the conservation of migratory shorebirds in this region of the Pacific Flyway. These include scaling up investments in habitat programs, adjusting their timing of implementation, and adapting them to new geographies. Below we offer initial guidance on how this might be done, while recognizing some of the challenges.

Scaling up investments in shorebird habitat

Our results reinforce the conclusions of the CVJV (2020) that advancing the conservation of shorebirds in the Central Valley requires an expansion of habitat, even if the focus is just on supporting the assumed baseline population. Currently, post-harvest flooded rice fields are estimated to contribute >50% of the food energy consumed by shorebirds over the non-breeding season (Figure 10 in Dybala et al., 2017). They are a critical resource to shorebirds and other waterbirds (Elphick & Oring 1998, 2003, Eadie et al., 2008); however, when conventionally managed, they provide shorebird habitat only from October

into March. Thus, they do little to meet the habitat needs during the shortfall periods identified in this study. Alternative rice field management practices can help overcome this limitation in rice (Golet et al., 2018, Sesser et al., 2018), as can flooding of other cover types including fallow fields, and managed wetlands. Souza-Cole et al. (2020) found that the gradual drawdown of San Joaquin Valley seasonal wetlands in spring provided over twice as much shorebird habitat as wetlands that were traditionally managed. As well, these wetlands supported 11 times more shorebirds during peak migration. However, Parrott and Quinn (2016) reported reduced production of swamp timothy (*Crypsis schoenoides*), an important waterfowl food, in wetlands managed with this practice, although watergrass (*Echinochloa crusgalli*) appeared unaffected. Expanding semipermanent wetlands provides an attractive additional option for increasing shorebird habitat given that they are typically drawn down in July and August (Duffy and Kahara 2011), when shorebird habitat shortfalls commonly occur (Dybala et al., 2017; this study). Plus, they have the added benefit of providing summer brood habitat for waterfowl, which is in short supply in the Central Valley (CVJV, 2020).

Restoring managed wetlands presents an attractive solution to meeting shorebird habitat needs because it provides a long-term conservation solution and may offer multiple ecosystem service benefits such as water quality improvements, flood damage reduction, groundwater recharge, and carbon storage (CVJV, 2020; Gardner & Finlayson, 2018; Hemes et al., 2019). However, temporary habitats can also provide multiple benefits (Rohde et al., 2019), and there is no a priori reason that agricultural or “working” lands, including those in private ownership, cannot be managed for long-term habitat value (e.g., TNC’s Staten Island Preserve, California, Shuford et al. [2015]). Agricultural lands have the advantage of providing significant income to farmers, but managed wetlands tend to support a more diverse assemblage of wildlife (Shuford et al. 2019) and have higher shorebird food energy content (Dybala et al., 2017). Because these different habitat types each have distinct advantages, they can effectively complement one another for the benefit of both people and nature (Boulton et al., 2016; D’Aloia et al., 2019).

Adjusting the timing of habitat provided

Because supporting the baseline population is a prerequisite to expanding it, in the near term, fall should be prioritized over spring by habitat programs. Habitat shortfalls were of larger magnitude and much more consistent in fall compared to spring under the baseline population

scenario, yet habitat incentive programs typically focus on providing habitat in spring (MBCP, 2014). That shorebird densities and species richness in incentive program fields were significantly higher in fall compared to spring (Golet et al., 2018), supports the idea that fall provides the greater return on investment.

Fine tuning of the seasonal provisioning of habitat is also needed. Relative to what we observed in our study, habitat should be created earlier in fall (July–August), and later in spring (April). This would help overcome shortfalls by better aligning projects with the migration phenology of the birds. There can be challenges to doing this, however. In early fall, most agricultural crops are still in production, although there are exceptions (e.g., winter wheat, sunflowers, safflower). High early fall temperatures can cause increased rates of evaporation (necessitating greater water allocations), rapid weed growth (reducing habitat value), and production of mosquitos (potentially spreading disease, Kovach and Kilpatrick [2018]). Allocating limited water supplies to early fall flooding may also conflict with best management practices for waterfowl (Petrie et al., 2016), although other species such as rails have been shown to benefit (Fournier et al., 2019). Providing habitat in late spring can be difficult due to delays it can cause in planting the next year's crop. Both spring and fall timing constraints are eliminated, however, in agricultural fields that are temporarily idled, a practice that is common in organic rice production and that may also have benefits in conventional farming (Norsworthy et al., 2012).

Adapting habitat programs to new geographies and landscapes

Increased investments in shorebird habitat in the Central Valley should be tailored to specific opportunities found in different regions. Shorebird species are not distributed evenly across the valley, and species have distinct habitat preferences (Shuford et al., 1998). While shorebirds can make some range adjustments to adapt to changing conditions (e.g., Barbaree et al., 2018), restoring habitat types that species are adapted to, in regions where they have recently occurred, is likely to be the most effective strategy for expanding populations, although planning efforts should also account for expected range shifts due to climate change (Jones et al., 2016; Moilanen et al., 2014). Adapting incentive programs to different geographies presents opportunities to meet the varying needs of people as well. For example, strategic placement of seasonal waterbird habitat can be an effective way to restore locally depleted groundwater aquifers (Rohde et al., 2020).

Most previous shorebird habitat incentive programs have focused on Sacramento Valley rice farms (Reiter et al., 2018), yet shorebirds are known to use a much wider array of habitats across the entire Central Valley (Fleskes et al., 2012; Shuford et al., 1998). For example, although Dunlin, Killdeer (*Charadrius vociferus*), and Greater Yellowlegs (*Tringa melanoleuca*) appear most common in Sacramento Valley agricultural fields, American Avocet, Wilson's Phalarope, Red-necked Phalarope, and Black-necked Stilt (*Himantopus mexicanus*) tend to concentrate in evaporation ponds in the Tulare Basin, and managed wetlands elsewhere in the valley (Barbaree et al., 2020; Shuford et al., 1998). It follows then that these other landscapes should also be targeted for implementing habitat projects, to the extent that it is not cost prohibitive to do so.

There is also considerable temporal variation in habitat use by shorebirds that should be considered (Robinson et al., 2020). For example, Western Sandpiper is most common in shallow saline wetlands in the San Joaquin Valley in winter, but in spring they utilize a wider range of wetland and agricultural habitat types throughout the Central Valley (Shuford et al., 1998). Changes in shorebird use patterns also occur across years. During the 2013–2015 drought, the San Joaquin and Tulare basins experienced greater declines in open water (Reiter et al., 2018) and bird abundance (Barbaree et al., 2020), than the Sacramento Valley, and certain species are disproportionately found in these regions. Thus, to be most effective, the specific geographic focus of habitat projects may need to shift both seasonally and across years.

Applying dynamic conservation to habitat projects

Although our results demonstrate that there are times when more habitat is always needed, they also reveal some variability in needs from year to year. To address this variability, a dynamic approach to habitat management can be implemented. This involves scaling the amount of habitat created to match the varying needs of the birds, which is an effective way to maximize return on investment (D'Aloia et al., 2019; Reynolds et al., 2017). For example, more habitat can be prioritized in the fall following dry years, and in spring if seasonal rains do not come. Recent advances in characterizing near real-time flooding patterns (e.g., Reiter, Elliott, et al., 2015) are helpful in assessing spring habitat conditions, however, considerable uncertainty remains in predicting future habitat needs, largely due to difficulty in forecasting rainfall. Our experiences suggest that further development of ecological forecasting tools, increased

flexibility in how habitat projects are implemented, and a successful scaling mechanism are important next steps for fulfilling the promise of dynamic habitat management for shorebirds in the Central Valley.

CONCLUSIONS

Wetlands worldwide are in decline and vulnerable to changing climate and human impacts (Gardner & Finlayson, 2018), with potentially dire consequences for migratory waterbirds. Habitat incentive programs present a valuable opportunity to help impacted species, however, their effectiveness is often not rigorously evaluated (Kleijn & Sutherland, 2003). Our studies of shorebirds the Central Valley provide an exception. Previously we measured the success of implemented programs with intensive monitoring at the site level, and here we evaluated the effects of the programs at the landscape scale for different population sizes. Further, we compared habitat needs with and without the contribution of the incentive programs over a series of years with strikingly different environmental conditions, including extreme wet and dry conditions. This work thus addresses the critical research need of better understanding the effects of drought on non-breeding shorebirds in the Central Valley (Barbaree et al., 2020; Reiter et al., 2018; Reiter, Elliott, et al., 2015).

Our results do not highlight how much worse habitat conditions were for shorebirds during drought, but rather how consistently bad conditions were during certain seasons, irrespective of whether it was a wet or dry year. This finding underscores how highly managed the hydrological system is in the Central Valley, especially during early fall and late spring when our studies suggest migratory shorebirds need habitat most. These needs arise because water allocations in the Central Valley are driven more by policy decisions than by the natural patterns of water distribution and abundance (Grantham & Viers, 2014) that the birds evolved to depend upon. In this way, the Central Valley may be similar to many other developed agricultural regions that formerly contained vast wetland areas. From a conservation standpoint, the highly engineered nature of water storage and delivery also means that the timing of water distribution can potentially be changed to improve conditions for the birds, provided there is sufficient societal will.

The consequences of the unmet habitat needs that our study suggests exist for migratory shorebirds in the Central Valley are largely unknown, but certainly may include declining population sizes, as have recently been documented for shorebirds on both regional (Stenzel & Page 2018; Warnock et al., 2021) and continental scales

(Rosenberg et al., 2019). Finally, our finding of increased habitat shortfalls in recent years emphasizes the need to create additional habitat in the near term. Otherwise, this region may become a climate-induced resource bottleneck (sensu Maron et al., 2015) of the Pacific Flyway.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Dybala & Golet, 2022) are available in Zenodo at <https://doi.org/10.5281/zenodo.6525519>.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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