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Informing wetland management with waterfowl movement and sanctuary use responses to human-induced disturbance

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ABSTRACT

Long-term environmental management to prevent waterfowl population declines is informed by ecology, movement behavior and habitat use patterns. Extrinsic factors, such as human-induced disturbance, can cause behavioral changes which may influence movement and resource needs, driving variation that affects management efficacy. To better understand the relationship between human-based disturbance and animal movement and habitat use, and their potential effects on management, we GPS tracked 15 dabbling ducks in California over ~4-weeks before, during and after the start of a recreational hunting season in October/November 2018. We recorded locations at 2-min intervals across three separate 24-h tracking phases: Phase 1) two weeks before the start of the hunting season (control (undisturbed) movement); Phase 2) the hunting season opening weekend; and Phase 3) a hunting weekend two weeks after opening weekend. We used GLMM models to analyze variation in movement and habitat use under hunting pressure compared with 'normal' observed patterns prior to commencement of hunting. We also compared responses to differing levels of disturbance related to the time of day (high - shooting/~daytime); moderate - non-lethal (~crepuscular); and low - night). During opening weekend flight (% time and distance) more than doubled during moderate and low disturbance and increased by ~50% during high disturbance compared with the pre-season weekend. Sanctuary use tripled during moderate and low disturbance and increased ~50% during high disturbance. Two weeks later flight decreased in all disturbance levels but was only less than the pre-season levels during high disturbance. In contrast, sanctuary use only decreased at night, although not to pre-season levels, while daytime doubled from ~45% to >80%. Birds adjust rapidly to disturbance and our results have implications for energetics models that estimate population food requirements. Management would benefit from reassessing the juxtaposition of essential sanctuary and feeding habitats to optimize wetland management for waterfowl.

1. Introduction

Land management for wildlife is aimed at preventing population declines and maintaining ecological function, and is supported by a good understanding of habitat and resource requirements (Bettinger et al., 2001; Loomis, 2002). Needs vary by species and ecosystem, but accurate movement and habitat-use information can help inform management decisions regarding distribution and provision of essential resources (DeFries et al., 2007). Strategies to address conservation and management of mobile species are complicated by their spatially and temporally dynamic distributions (Runge et al., 2014). Species movements must be incorporated when developing management objectives but the knowledge of when, where and why species move is often lacking (Allen and Singh, 2016). Management is further complicated by anthropogenic activities that disturb animals in their natural environment, altering movements and habitat use. Disturbance is associated with other negative effects such as, reduced reproductive output and breeding success, and population declines (e.g. Carney and Sydeman,

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1999; Caro, 1999; Stankowich, 2008).

One significant source of disturbance is recreational hunting, which poses an enormous risk to animals' safety (e.g. Cox et al., 1998; Madsen and Fox, 1995; Tamisier, 1985) and animals have been found to react strongly to humans in areas with high hunting pressure (Caro, 1999; Stankowich, 2008). Globally hunted waterfowl are a highly mobile taxa whose normal daily activities are affected in multiple ways by hunting disturbance through changing patterns of movement, distribution and habitat use (Casazza et al., 2012; Madsen and Fox, 1995). Birds are more likely to take flight (Casas et al., 2009; Pease et al., 2005), fly greater distances (Dooley et al., 2010a; Fleskes et al., 2005) and delay crepuscular evening flights (Miller, 1985; Paulus, 1988; Tamisier et al., 2003). Birds can increase daytime use of sanctuaries, be displaced from preferred roosting and feeding habitats (Davis and Afton, 2010; Paulus, 1984; St. James et al., 2013), and feeding can be curtailed (Korschgen et al., 1996; Morton et al., 1989).

Prior research into disturbance effects on animal movement has been observational or based on low frequency tracking (2 locations per day; e.g. Fleskes et al., 2005; Madsen and Fox, 1995; Tamisier et al., 2003), and therefore could not quantify movements beyond line of sight. Fleskes et al. (2005) determined that ducks flew farther when hunted than not, but could not estimate distance or time flying. Single-disturbance event effects, or responses over longer time-scales (e.g. one or more hunting seasons), have been evaluated (Davis and Afton, 2010; Dooley et al., 2010a; St. James et al., 2013) but few assessed immediate effects of intense disturbance or resulting behavioral variation (Casas et al., 2009; Dooley et al., 2010b). Disturbance intensity varies depending on the activity. Animals react to humans on foot (Pease et al., 2005; Wolf and Croft, 2010) and ducks react most strongly to loud noises like gunshots (Korschgen and Dahlgren, 1992; Meltofte, 1982). However, these factors are often omitted in developing management plans.

In North America, waterfowl land and resource management has primarily focused on ensuring sufficient suitable habitat, hunt-free sanctuaries and optimizing food availability (Central Valley Joint Venture, 2006; Environment Canada and US Department of the Interior, 2018, 1986). Waterfowl population food requirements are largely estimated based on information derived from bioenergetics models such as the agent-based 'SWAMP' model or the spatially implicit 'TRUEMET' model that calculate individual energy-use (Central Valley Joint Venture, 2006; Miller et al., 2014). If values used in these calculations, such as time flying, are inaccurate, waterfowl food requirements may require re-evaluation. Flight is more energetically expensive than other forms of locomotion (Nudds and Bryant, 2000; Wooley and Owen, 1978), so measurable flight increases due to disturbance (e.g. via distance or time flying) could affect health or survival through increased energetic requirements (Madsen and Fox, 1995; Pease et al., 2005). Waterfowl experience considerable human-induced disturbance via annual waterfowl hunting seasons that are often protracted for multiple months and which are likely to impact behavior. If so, disturbance may need to be incorporated as an additional parameter in energetics models to refine energy-use calculations and improve management by more accurately estimating population resource needs (Gill et al., 2001). Furthermore, if waterfowl vary use of specific managed habitats such as sanctuaries, in response to the noise and disturbance of hunting activity (Casazza et al., 2012; Madsen and Fox, 1995), management of these resources may also require reconsideration.

The aim of this study was to understand how duck movement and habitat use might vary due to human-induced disturbance (caused by hunting) and use this information to improve management of essential wetland resources for large waterfowl populations. The abrupt escalation in human disturbance at the onset of the annual waterfowl hunting season offers an ideal opportunity to quantify waterfowl behavioral responses to various levels of disturbance. Therefore, we conducted a high frequency GPS tracking study of California dabbling ducks to compare variations in patterns of movement and habitat use during three tracking phases: before, during and after commencement of hunting. We could then test whether movements and use of sanctuaries (and hence, energy use and resource intake requirements) changed with commencement of hunting disturbance on the season opening day compared with observations during pre-season tracking, and in the final phase of tracking after the commencement of hunting, and how these factors varied according to the level of disturbance.

Specifically, we expected that flight (time spent flying/distance flown) would increase on opening day. We also expected further variation in movement during the 3rd tracking weekend 2 weeks after opening day, as birds acclimated to the noise and activity of hunting pressure. In addition, we expected time in sanctuaries during the day (highest disturbance) would progressively increase over the three tracking phases as ducks became increasingly habituated to and avoided hunting disturbance. Variations in movement and habitat use have significant implications for resource demands and habitat requirements and a better understanding of these factors supports enhancements to wetland management and increases its efficacy.

2. Materials and methods

2.1. Study area and species

To measure fine-scale spatio-temporal movement responses to disturbance, we tracked individuals of three of California's most numerous dabbling duck species: *Anas acuta (*Northern pintail, hereafter pintail), *A. platyrhynchos* (mallard) and *Mareca strepera* (gadwall); across California's Central Valley. Capture and marking of ducks with GPS occurred primarily in Suisun Marsh, between January 2017 and September 2018. We captured ducks with handheld dip nets, baited funnel traps and rocket nets (Drewien and Clegg, 1992; Haramis et al., 1982; Schemnitz et al., 2009), during spring (March to June) and fall (September to October) at Grizzly Island State Wildlife Area (SWA; 38.138306°, −121.978056°) and surrounding private properties within Suisun Marsh. Gadwall and mallard females nesting on Grizzly Island SWA were found using standard nest dragging techniques (McLandress et al., 1996) while pintail were captured upon arrival in the fall using rocket nets. Ducks were individually identified with numbered aluminum U.S. Geological Survey Bird Banding Lab leg bands, and aged based on feather and molt plumage (Carney, 1992), as hatch-year (HY), second year (SY), after second year (ASY) or after-hatch-year (AHY). Only adult (not HY) birds received GPS transmitters and therefore would have previously experienced at least one hunting season.

2.2. Electronic tracking

We used **s**olar-powered, remotely programmable, Ornitela® Ornitrack-15 GPS-GSM electronic transmitters (~5 m location accuracy; 58 × 25 × 14 mm; 15 g), fitted with a 3 mm foam base pad. Devices were attached to back-mounted body harnesses constructed of 9.5 mm automotive elastic and knotted, which added 1–1.25 g to the deployment weight. Ducks were released at the location of capture after a handling time of <30 min. To ensure the deployment weight was within the accepted 3% body weight limit for birds (Cochran, 1980; Kenward, 2001), we assessed each individual's weight and body size with morphometric measurements. GPSs store data onboard until location data (with date-time stamp) can be transmitted via cellular GSM text message when in network range, and as battery power and GSM signal strength allowed. In general, GPS location resolution varies dependent on battery life between 30 min and 6 h. As location interval increases battery life depletes more rapidly resulting in lower location frequency.

2.3. Tracking phases

The 2018 annual California waterfowl hunting season commenced on Oct 20th (ended Feb 6th) and we tracked ducks across a ~4-week period in October and November 2018 with GPS-GSM devices set to obtain precise locations at 2-min intervals during three separate 24-h phases of tracking: 1) ‘pre-season’; 2) ’opening day’ and 3) ‘during the season’. Phase 1, the ‘pre-season’ phase (October 8–11th) was our control during which we tracked 32 individuals, represented ducks’ patterns of movement and habitat use when disturbance is very low and there is no hunting. Phase two (‘opening day’), tracked 25 individuals on the opening day of the hunting season (October 20th) when human-induced disturbance increases from to the highest levels. Phase three (‘during the season’) tracked 22 individuals two weeks later, on November 4–5th. The first pulse of wetland flooding occurs in early October to attract ducks, followed by a second pulse in late November to encourage rice harvest decomposition (Central Valley Joint Venture, 2006; Elphick and Oring, 1998) thus minimizing habitat variability across the study period. Finally, we obtained additional tracking data from 10 individuals on day 2 of opening weekend (October 21st). We designated this as phase 2.1 and used this to test whether birds would vary movement and space-use across the shorter-term of two successive days. Weather was consistently fine with low winds across all days of tracking in all three phases.

By comparing behavior across phases, we can assess how movement changes according to the occurrence of disturbance and whether ducks adjust to disturbance over time. We removed any individuals with less than 20 h of tracking data and any tracked in the Klamath basin/Southern Oregon/Northern California (SONEC) where the hunting season commenced too early for us to obtain pre-season data, to arrive at a final dataset of 15 individual ducks (Table 1; Fig. 1). We classified all location data with the individual bird identifier (Bird ID), species, sex, basin (Suisun Marsh, Sacramento Valley including Delevan and Colusa Wildlife refuges, Delta, San Joaquin and the rest of California and Nevada) and the day and phase during which it occurred. All locations were identified in UTC and local time zones allocated to calculate sunrise and sunset and time (in minutes) from each.

2.4. Disturbance intensity

To determine if the type or intensity of disturbance affected ducks differentially, we classified disturbance into three categorical levels: 1) High - the period during which hunters can shoot (from 30 min prior to sunrise until sunset); 2) Moderate - the period 1.5 h prior to commencement of shooting, and 1 h after cessation of shooting, when human activity on the landscape causes non-shooting related disturbance (e.g. setting up or removing hunting equipment and accessing hides); and 3) Low - the period during the night from 1 h after sunset to 1.5 h prior to sunrise when disturbance is lowest with little to no human activity and no human derived mortality risk. Each 2-min interval between successive locations constituted a ‘step length’ on the movement track and we attributed each with the applicable disturbance level. Although these levels of disturbance do not apply during phase 1 when there is no hunting, we use the same descriptions to compare among phases.

2.5. Movement behavior

To classify behavior, we calculated the speed and distance moved for each step length. Speeds greater than 5 kmh^{-1} were classified as flight, between 0.6 and 5 kmh^{-1} classified as swimming or walking and below 0.6 kmh^{-1} as resting (Cooke, 1933; Hedenström and Alerstam, 1995; Usherwood et al., 2008). We analyzed time flying across phase and disturbance levels to determine the times of day that ducks made between area movements (e.g. foraging to roosting areas) and if hunting disturbance invoked flight responses. Time flying can be used to quantify duck responses to disturbance, but if flights were shorter than 2-min, or speeds varied, this would cause variations in distances flown. Therefore, we included all types of movement (resting, swimming/walking and flying), when assessing how distance moved differed among phase and disturbance level combinations. These calculations and classifications were made using the adehabitatLT package (Calenge, 2015) in R (R Core Team, 2019).

2.6. Use of sanctuary areas

To determine if ducks were avoiding disturbance by using sanctuary areas where hunting is prohibited, we classified all bird locations according to whether they occurred within or outside of known sanctuaries. For the purposes of this study, sanctuaries are either administrative (official closed zones/refuges), or defacto, such as municipal boundaries or private lands in which hunting is known not to occur. If a point was within a municipal boundary (TIGER; U.S. Bureau of the Census., 2018) it was classified as sanctuary because hunting is prohibited within the boundaries. Public lands were determined by the Protected Areas Database of the United States (U.S. Geological Survey, 2020) an inventory of public lands. Points within public lands were classified as huntable or sanctuary based on hunting maps provided by the land managing agency or review from federal and state land managers. All points outside of municipal boundaries or within public lands were considered huntable except a few in known privately managed sanctuaries which were classified as sanctuary (see Fig. 1). The classifications were conducted in ArcGIS 10.7 for Desktop (Esri, Redlands, CA, USA) and R (R Core Team, 2019) using the using the simple features package (Pebesma, 2018). One individual never spent time in a known sanctuary area, so we removed this bird from the sanctuary-use analysis so as not to bias parameter estimates, leaving a sample size of 14 ducks.

Table 1

Data for 15 tracked California ducks including total number of locations and number of flights (2-min intervals) during 3 main phases of tracking (phase 1 = before hunting season; phase 2 = opening day; phase 3 = during the season) and data for a subset of birds also tracked across the 2nd day of the opening weekend (phase 2.1).

Bird ID	Species	Phase 1		Phase 2		Phase 2.1		Phase 3	
		# GPS	# Flights	# GPS	# Flights	# GPS	# Flights	# GPS	# Flights
180622	Mallard	657	26	721	6	NA	NA	721	6
180634	Pintail	720	16	721	14	719	4	719	58
180638	Pintail	713	22	721	9	659	17	720	15
180640	Pintail	661	10	721	23	718	21	721	9
180647	Gadwall	718	5	721	6	NA	NA	719	11
180655	Mallard	720	7	600	4	NA	NA	721	15
180656	Mallard	721	4	721	4	719	NA	721	2
180666	Gadwall	716	10	721	3	719	3	721	6
180674	Pintail	660	14	721	11	659	39	721	10
180675	Pintail	720	20	720	32	719	23	721	12
180676	Pintail	667	10	721	58	720	10	720	14
182138	Pintail	706	12	720	23	NA	NA	718	16
182141	Pintail	607	1	721	10	NA	NA	721	17
182143	Pintail	718	13	721	68	655	9	721	4
182148	Pintail	721	8	721	63	598	10	720	14

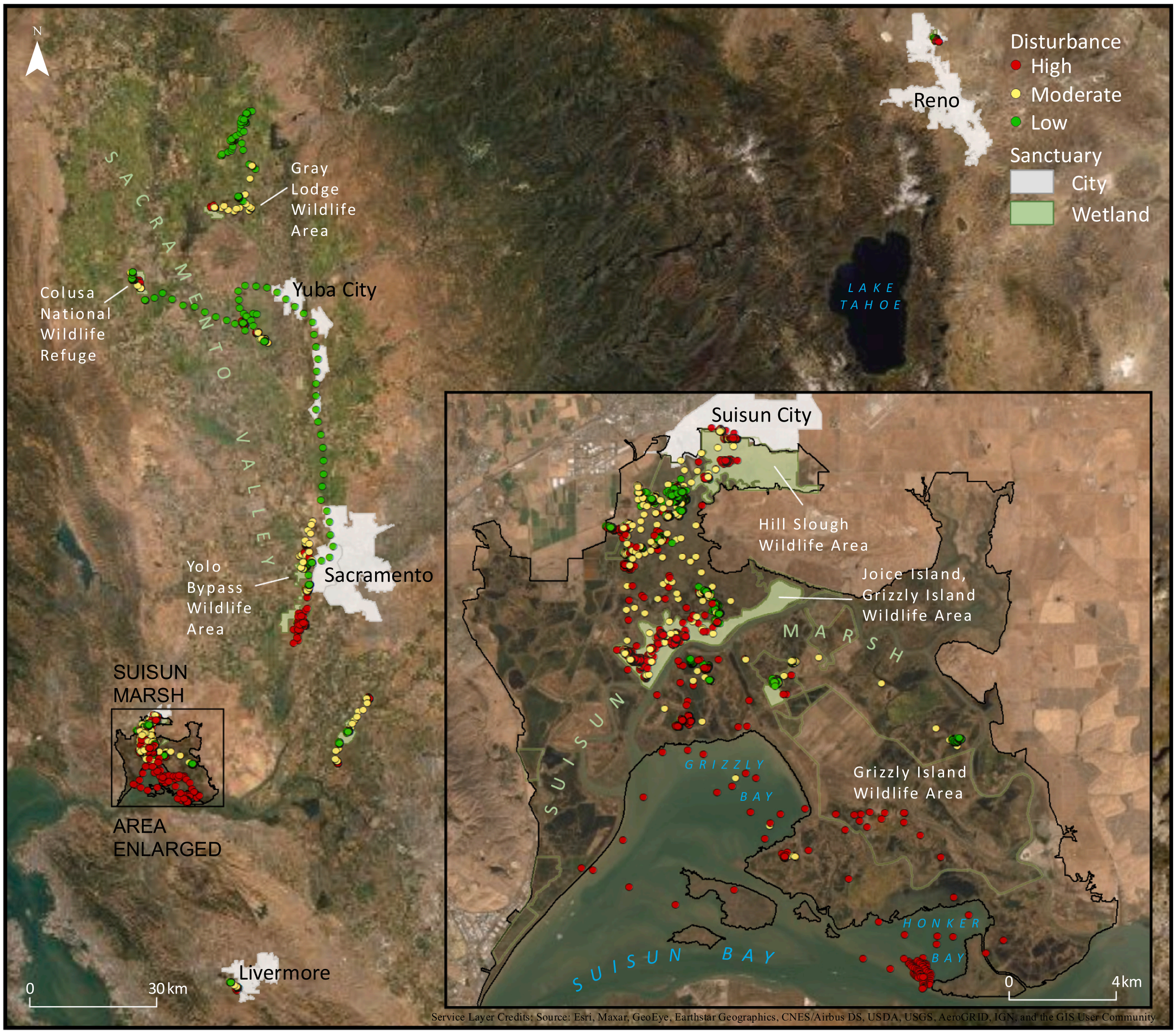

Fig. 1. Map showing all 2-min interval GPS locations for each of our 15 ducks tracked across areas of California and Nevada. All locations across the 3 phases of tracking (1 = before hunting season; 2 = opening day; 3 = during the season) are colored according to 3 disturbance levels: low (green; night), moderate (yellow; 1.5 h before lethal activity and 1 h after) and high (red; shooting). Although disturbance does not apply during phase 1 when there is no hunting, we use the same descriptions to compare among phases. Only known sanctuary areas used by ducks in our tracking study are displayed. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2.7. Statistics

We analyzed movements by calculating the proportion of time flying (2-min step lengths), the total distance moved (all movements: resting, swimming/walking and flying), and the proportion of time in sanctuary areas, in each of our three phase (before hunting season, opening day of hunting season, and during the hunting season) and disturbance level (low, moderate, high) combinations. We used generalized linear mixed models (GLMM) with Laplace approximation and binomial responses when modeling the proportion of time flying (flight = 1, not flight = 0) and in sanctuary areas (in sanctuary = 1, not in sanctuary = 0). We used a gamma distribution model with loglink function for distance moved. Phase and disturbance level were specified as fixed effects and individuals (bird ID) as a random effect. We compared models of the interactive, additive and individual effects of phase and disturbance level on each of the response variables using the bias-corrected version of Akaike's Information Criterion for small sample sizes (AICc; Burnham and Anderson, 2003). Models were run with the 'glmer' function in the 'lme4' (Bates et al., 2015) and 'emmeans' (Lenth et al., 2020) packages in R. We used a priori criteria of AICc weights (wAICc) $\geq$ 0.90 to designate one of the four models as having the most support. If wAICc were <0.90, parameter estimates were derived by model averaging (Burnham and Anderson, 2003). Estimates and their 95% confidence limits were back transformed where applicable. To understand the patterns of movement across the entire duration of each time period associated with the three disturbance levels in all three phases of tracking we produced circular distributions of all flighted step lengths and locations in sanctuaries according to the time of day of occurrence. Data are available in the U.S Department of the Interior and U.S. Geological Survey's ScienceBase (McDuie et al., 2021).

3. Results

3.1. Proportion of time flying

California ducks of three species (n = 15) tracked at 2-min intervals with GPS-GSM provided 31,922 locations to assess flight (Table 1). To determine if the level of disturbance caused these ducks to change their movement patterns, we tested the variation in time flying among phases and disturbance levels. The model with an interaction between phase and disturbance level for proportion of time flying was completely supported (ΔAICc = 22.7; wAICc = 1; Table 2). Prior to hunting (pre-

Table 2
GLMER model results testing the proportion of time flying for ducks (n = 15) tracked in California in 2018. The strongest model was the interaction between the 3 phases of tracking and disturbance level (high, moderate and low). See supplementary materials for contrasts phases × disturbance levels and disturbance levels × phase.

	TIME FLYING					
	K	AICc	ΔAICc	AICcWt	Cum. Wt	LL
Interaction (Phase*Disturbance)	10	1144.1	0	1	1	−561.1
Additive (Phase + Disturbance)	6	1166.8	22.69	0	1	−577.1
Disturbance (only)	4	1217.9	73.87	0	1	−604.8
Phase (only)	4	1412.1	268.02	0	1	−701.9

season, phase 1) most flying time occurred near dawn and dusk (moderate) and little at night (low; SI Tables 1 and 2; Fig. 2). Two weeks later, on opening day of the hunting season (phase 2) the time flying increased 3 × and 2 × during the hours of low and moderate disturbance respectively (SI Tables 1 and 2; Fig. 2). Flight time was also higher on opening day during the high disturbance hours (~daytime; lethal activity/shooting), but the magnitude of the change was less (1.7%–2.5%; SI Tables 1 and 2; Fig. 2). By the third phase of tracking two weeks later, all disturbance levels showed less flight than phase 2, and both high and low disturbance flight had reduced below phase 1 levels (SI Tables 1 and 2; Fig. 2). Most flight occurred during moderate disturbance and this difference was greatest in phase 3 with at least 5 × flight more flight (5.7%) than in the other two disturbance classes (1.2% low & 1% high; SI Tables 1 and 2; Fig. 2).

Within each disturbance level, we summarized movements according to the specific hours they occurred, to understand the finer scale distribution of when flights occurred. The most noticeable increases in phase 2 were around 6–7:30 a.m., (moderate and high), midmorning (high) and in the late evening hours prior to midnight (low; Fig. 3). In phase 3, movement reduced from that seen in phase 2 and was more similar to the normal circadian patterns represented by phase 1 movements. However, there were fewer daytime flights and more nocturnal flights (Fig. 3).

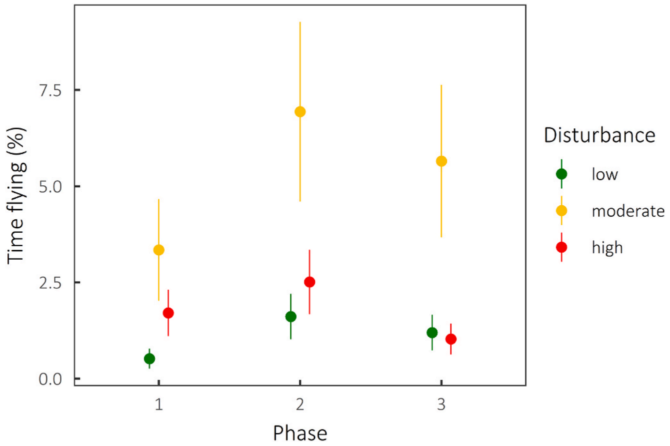

Fig. 2. Probability of California ducks (n = 15) flying during 3 phases of GPS tracking according to the disturbance level, presented with 95% CI. Phase 1 = before hunting season; 2 = opening day; 3 = during the season; colored according to 3 disturbance levels: low (green; night), moderate (yellow; 1.5 h before lethal activity and 1 h after) and high (red; shooting). Although disturbance does not apply during phase 1 when there is no hunting, we use the same descriptions to compare among phases. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.2. Behavioral variations

Individual variation in flight time among the 15 ducks was apparent (SI Fig. 2). Based on the random effect estimates, there was an indication of three groups; five that flew more than the others, four that did not demonstrate very much variation in the amount of time they flew, and six that flew less. The magnitude of variation among the ducks that flew more and those that flew less was similar, with the exception of one individual that flew notably less than the others (SI Fig. 2). The residuals were largely consistent with assumptions of linear models, though they were slightly skewed by the individual that flew less than the others (SI Fig. 2).

3.3. Distance moved

GLMER models testing variation in distance moved for all movement types (resting, swimming/walking and flying) showed that the interaction model between phase and disturbance had the lowest AICc value among the four models for distance moved (Table 3). The level of support for it was only marginally better than the additive model though (ΔAICc = 1.70; wAICc = 0.68; Table 3), therefore, we used model averaging to derive parameter estimates and predicted values. In phase 2, all disturbance levels showed significantly increased movement distance: >40% in daytime, 230% at night and 120% during moderate disturbance (SI Tables 1 and 2; Fig. 4). By phase 3, distances moved were lower in all disturbances (61% less in high, 47% less in low and 11.5% less in moderate) than the previous phase, but only during high disturbance had movement fallen below that (almost half) of their circadian pattern of phase 1. Nocturnal and moderate periods were still 7% and 94% greater (SI Tables 1 and 2; Fig. 4).

3.4. Sanctuary use

We assessed variation in habitat use, in response to disturbance, by testing differences in sanctuary use for 14 individual ducks among phases and disturbance levels (one never used sanctuary). There was complete support (ΔAICc = 20802.3; wAICc = 1; Table 4) for the model with an interaction between phase and disturbance level for proportion of time in sanctuaries. Across phases, sanctuary use was consistently the greatest during the day (high disturbance) and least at night (Fig. 5), but the proportion of time differed among phases. Use of sanctuaries was always significantly greater in phase 2 than 1 but when comparing phase 3 with 2, only use during the day increased, while night use decreased significantly. Before the hunting season commenced (phase 1) sanctuary use during moderate and low disturbance was similar (13% and 12% respectively) while daytime use was 3 × greater with ducks spending almost half their day in sanctuaries (SI Tables 1 and 2; Fig. 5). During phase 2 sanctuary use during the daytime had increased by 50% and use in moderate and low disturbance periods more than tripled. The moderate disturbance level in phase 2 showed the greatest magnitude of increase with use more than 2.5× greater than phase 1 (SI Tables 1 and 2; Fig. 5). By phase 3, two weeks after commencement of hunting sanctuary use during the daytime had doubled compared with phase 1 and ducks were spending almost the entire day in sanctuaries. Similarly, moderate disturbance use, while only slightly increased over phase 2, had almost tripled over phase 1. Only under low nocturnal disturbance was sanctuary use lower than phase 2 but not as low as pre-season (phase 1) use (SI Tables 1 and 2; Fig. 5).

The summary of time in sanctuaries by hour of the day for the 14 individuals that used sanctuaries shows that duck use of sanctuaries (refuges where no hunting is allowed, and disturbance is minimal) in phase 2 was generally greater than phase 1, regardless of time of day. Contrary to time flying, phase 3 use increased further at most times except the early hours of the morning during low disturbance, when usage most closely reflected the circadian patters of phase 1 (Fig. 6).

Fig. 3. Flighted movements according to time of day of California ducks (n = 15) during 3 phases of GPS tracking according to the disturbance level. Phase 1 = before hunting season; 2 = opening day; 3 = during the season; colored according to 3 disturbance levels: low (green; night), moderate (yellow; 1.5 h before lethal activity and 1 h after) and high (red; shooting). Although disturbance does not apply during phase 1 when there is no hunting, we use the same descriptions to compare among phases. Time of day is Pacific time (PT) – daylight savings time for phases 1 & 2 and standard time for phase 3. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 3

GLMER model results testing total distances moved by ducks (n = 15) tracked in California in 2018. The strongest model was the interaction between the 3 phases of tracking and disturbance level (high, moderate and low). See supplementary materials for contrasts: phase × disturbance levels and disturbance levels × phase.

	DISTANCE MOVED					
	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Interaction (Phase*Disturbance)	11	832.23	0	0.68	0.68	−404.04
Additive (Phase + Disturbance)	7	833.92	1.7	0.29	0.97	−409.52
Disturbance (only)	5	838.62	6.4	0.03	1	−414.08
Phase (only)	5	843.32	11.09	0	1	−416.43

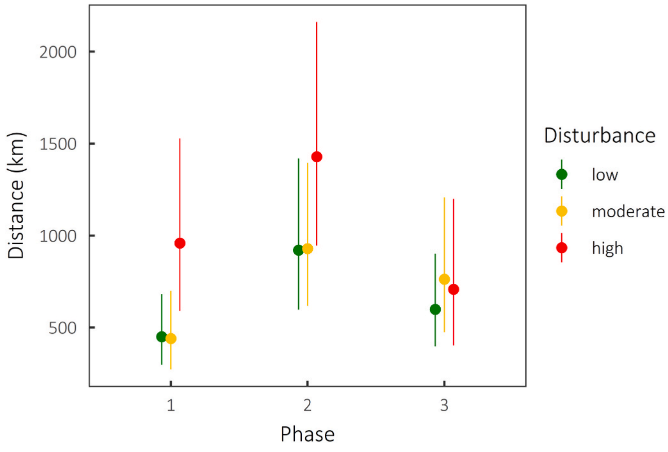

Fig. 4. Total distances moved (km) across all 2-min step lengths (resting, swimming/walking, flying) by California ducks (n = 15) during 3 phases of GPS tracking according to the disturbance level, presented with 95% CI. Phase 1 = before hunting season; 2 = opening day; 3 = during the season; colored according to 3 disturbance levels: low (green; night), moderate (yellow; 1.5 h before lethal activity and 1 h after) and high (red; shooting). Although disturbance does not apply during phase 1 when there is no hunting, we use the same descriptions to compare among phases. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.5. Responses over 48 h

We tracked a sub-sample of 10 individuals on the two consecutive days of the hunting season opening weekend to see if behaviors changed within 48 h. The interactive model using phase × disturbance level for proportion of time flying was the most supported model (ΔAICc = 598.79; wAICc = 0.88; SI Table 3). Birds spent most time flying when disturbance was moderate, and they consistently flew less on the second day (Sunday October 21st - phase 2.1) than the first (Saturday October 20th - phase 2) but this was only significant in low and high disturbance (SI Tables 1, 2 and 3; SI Fig. 3a). The greatest proportional reduction occurred during the night (low disturbance) when ducks spent approximately 1/5th the amount of time in the air as the previous day. Flight during moderate disturbance on the second day was approximately half that of the previous day and when disturbance was high flight reduced from 2.7% to 1.6%. The interactive model using phase × disturbance level for proportion of time in sanctuaries was the most supported model (ΔAICc = 5476.96; wAICc = 1; SI Table 4). Ducks (n = 9) consistently increased the amount of time within sanctuary areas regardless of the level of disturbance across the opening weekend of hunting (SI Tables 1, 2 and 4; SI Fig. 3b). Ducks always spent most time in sanctuaries during the high disturbance daytime, and this is when the most marked increase occurred with time in sanctuaries increasing from 70% to almost 100% of time.

4. Discussion

By examining bird movements, before, during and after the commencement of a hunting season, we developed an understanding of how human-induced disturbance impacts waterfowl population management via elevated disturbance (noise and activity) significantly altering behavior and habitat-use. During the highest disturbance level (lethal impacts/gunshots) on opening day (phase 2) ducks doubled time flying (4%–7.9%) and distances moved increased 30% compared with pre-season tracking. Time flying during the nocturnal period tripled

Table 4
GLMER model results testing the proportion of time inside sanctuaries for waterfowl (n = 15) tracked in California in 2018. The strongest model was the interaction between the 3 phases of tracking and disturbance level (high, moderate and low). See supplementary materials for contrasts: phase × disturbance levels and disturbance levels × phase.

	TIME in SANCTUARIES					
	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Interaction (Phase*Disturbance)	10	20802.30	0	1	1	−10390
Additive (Phase + Disturbance)	6	21442.27	639.97	0	1	−10715
Disturbance (only)	4	23030.96	2228.66	0	1	−11511
Phase (only)	4	28282.01	7479.71	0	1	−14137

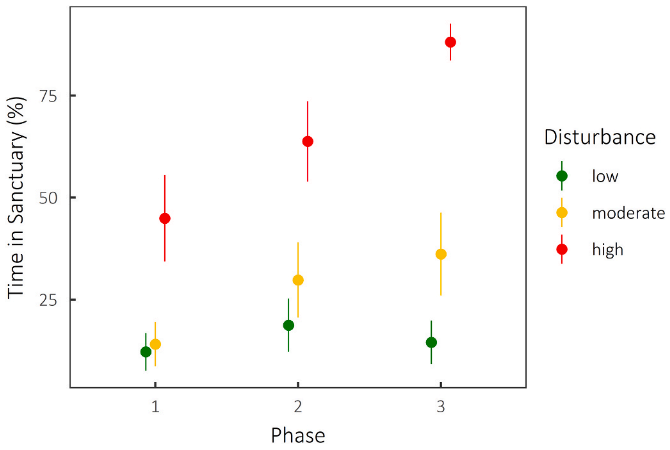

Fig. 5. The probability of ducks (n = 14) in California being in a sanctuary area during 3 phases of GPS tracking according to the disturbance level, presented with 95% CI. Phase 1 = before hunting season; 2 = opening day; 3 = during the season; colored according to 3 disturbance levels: low (green; night), moderate (yellow; 1.5 h before lethal activity and 1 h after) and high (red; shooting). Although disturbance does not apply during phase 1 when there is no hunting, we use the same descriptions to compare among phases. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(0.6–1.9%). An uncommonly lengthy, circuitous 97.8 km daytime flight by a single individual and a lengthy basin-switching nocturnal flight on opening day (Fig. 7), may have disproportionately influenced these results but neither would wholly explain the observed increases in flight (particularly during mid-morning, late afternoon and very early morning (Fig. 3). We also saw flight more than double during the moderate (non-lethal) disturbance time. Combined, these results indicates that both lethal (gunshots) and non-lethal (people moving about the landscape in boats or on foot), activities, all known to disturb ducks (Guay et al., 2014; Madsen and Fox, 1995; Meltofte, 1982), were the predominant drivers of observed movement variations across opening day.

By the time two weeks of hunting season had elapsed (phase 3), flight had reduced across the 24 h but had almost completely ceased during highest disturbance (daytime, only ~1.5%). Correspondingly, longer foraging flights were more concentrated across shorter timeframes in the low and moderate disturbance periods, indicating an increase in crepuscular and nocturnal activities compared with phase 1. That is, movement from day roost sanctuaries to foraging areas occurred later, after sunset, and movements back to roost sites occurred earlier, prior to the start of hunting, potentially imposing further limits on nocturnal foraging time. This shift in movement patterns indicates that California ducks, which are more likely than conspecifics in other regions (Bengtsson et al., 2014; Cox Jr and Afton, 1996) to perform longer daytime forage flights outside the hunting season (Casazza et al., 2012; Miller, 1986), modified their behavior in response to disturbance.

Ducks may have made this determination even more rapidly than over that two-week period. The reduced movement revealed across the two successive days of opening weekend (phases 2 vs 2.1) where ducks demonstrate a propensity to adjust to disturbance in a very short timeframe. Movement reductions could be due to fewer hunters, but this is unlikely at the beginning of the hunting season. Dwindling hunter numbers as the season progresses would diminish disturbance and potentially allow ducks to further adjust their behavior, but data on hunting activity were not available to quantify this. The pattern of reduced movement would also be consistent with improved foraging

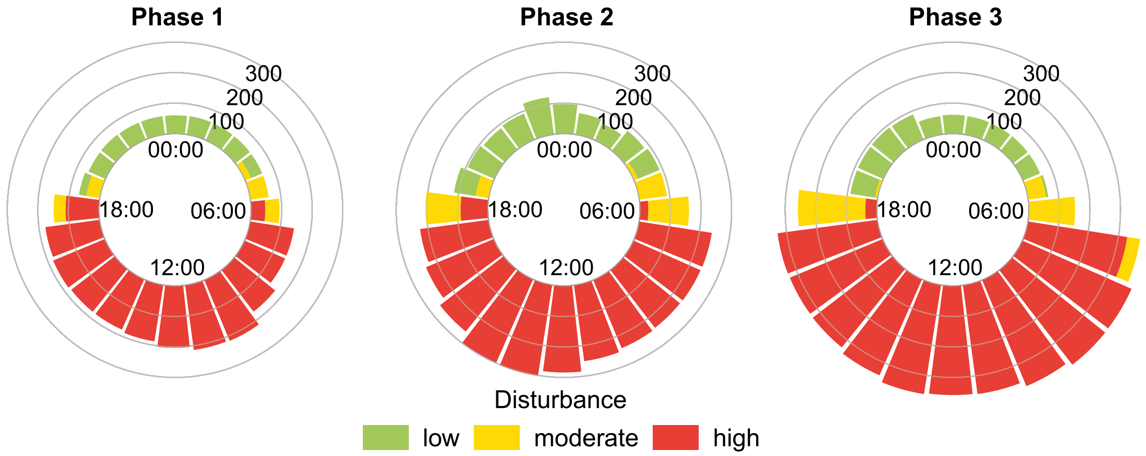

Fig. 6. Amount of time (no. of locations) California ducks (n = 14) spent in sanctuary areas according to time of day during 3 phases of GPS tracking. Phase 1 = before hunting season; 2 = opening day; 3 = during the season; colored according to 3 disturbance levels: low (green; night), moderate (yellow; 1.5 h before lethal activity and 1 h after) and high (red; shooting). Although disturbance does not apply during phase 1 when there is no hunting, we use the same descriptions to compare among phases. Time of day is Pacific time (PT) – daylight savings time for phases 1 & 2 and standard time for phase 3. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

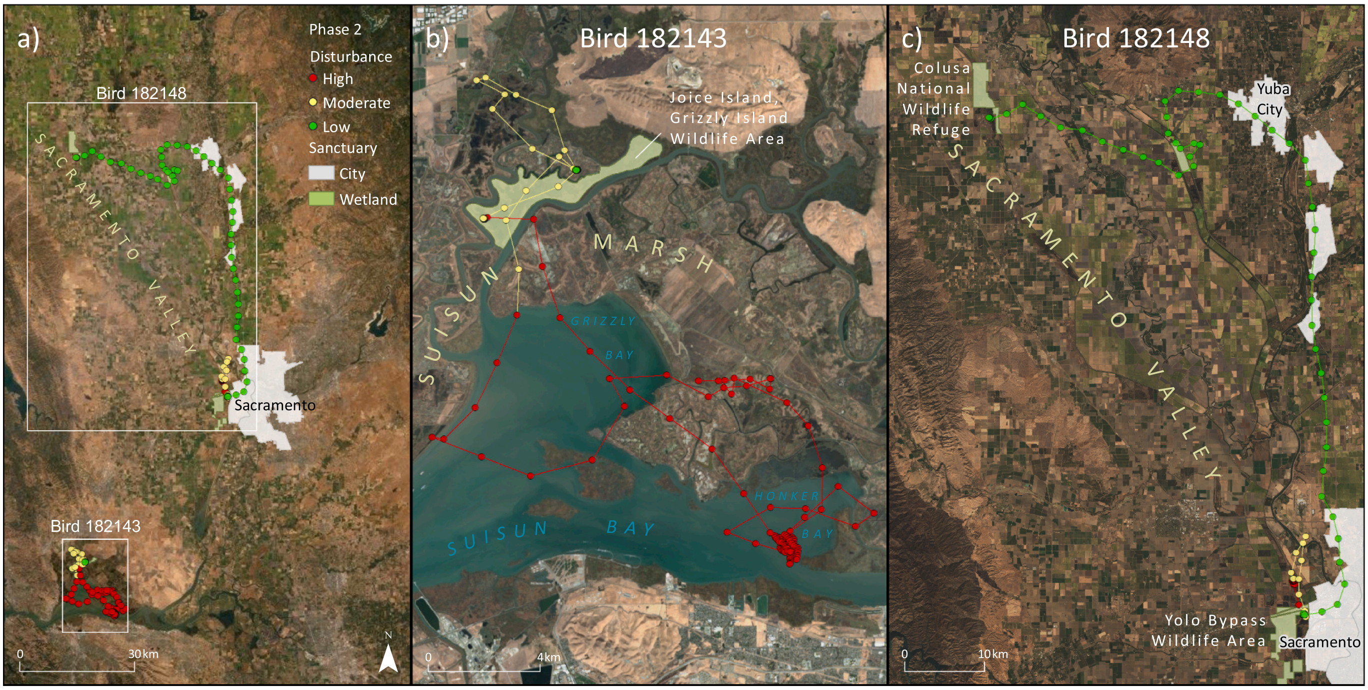

Fig. 7. Map showing sample GPS tracks from 2 California dabbling ducks that performed unusually long movements during phase 2 (opening day of the hunting season), demonstrating the complexity and detail of movement detectable with high frequency GPS data. Panel a) shows the locations of these two individuals in Northern California; b) is an individual in Suisun Marsh that flew 97.8 km between start and end points only ~5 m apart; and c) is an individual that began in Yolo Bypass and switched basis to move to Colusa Wildlife Refuge in Sacramento Valley. Locations are colored according to 3 disturbance levels: low (green; night), moderate (yellow; 1.5 h before lethal activity and 1 h after) and high (red; shooting). Sanctuary areas include city limits (white) which are not huntable and represent *defacto* sanctuary and wetland sanctuaries (green). Only sanctuary areas used by these individuals are displayed. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

efficiency. Whether these trends would continue throughout the hunting season is unclear and it would require a comprehensive, season-long movement study to disentangle these effects and determine if ducks continue to be impacted by disturbance. Regardless, persistent changed movement patterns indicate that human disturbance triggers a switch from pre-season diurnal foraging patterns to more nocturnal foraging activity (Miller, 1985, 1986), a phenomenon described in a variety of mammals (Gaynor et al., 2018). Low nocturnal use of sanctuaries supports this theory and implies that resources in sanctuaries do not fulfill waterfowl needs.

Sanctuaries are less often optimized for food resources compared with privately managed wetlands and agriculture (Central Valley Joint Venture, 2006), but consistently increasing daytime use of sanctuaries across the study illustrates their importance (~40% in phase 1 to >80% by phase 3). This would further constrain foraging time and could impact birds' ability to acquire adequate food resources that, combined with greater overall flight, may produce an energetic deficit that requires compensation (Bélanger and Bé). Waterfowl resource managers rely on accurate estimates of population food requirements that are derived from bioenergetics models such as 'SWAMP' and 'TRUEMET' models, which quantify individual energy use (Central Valley Joint Venture, 2006; Miller et al., 2014). These models are critical tools for developing management strategies directed at fulfilling food needs for the influx of millions of migrating waterfowl that overwinter in California. However, movement metrics currently used in models, such as percent of the day spent flying (2–6%; Paulus, 1988; Rave and Cordes, 1993; Wooley and Owen, 1978), do not account for the significantly greater flight of disturbed ducks. Flying is an energetically expensive form of locomotion (Nudds and Bryant, 2000; Wooley and Owen, 1978). Consequently, energetics models may underestimate waterfowl resource needs in areas where consistent disturbance is a factor. Although there is little evidence that California duck populations are food limited (Fleskes et al., 2016; McDuie et al., 2019), food/energy deficits could be more pronounced in areas of high disturbance. Given that hunting occurs for approximately 3 months of the year across broad geographic areas, management strategies may need to account for seasonal disturbance-related impacts to food requirements.

In California, waterfowl food requirements have been the long-term focus of management with seasonal wetlands managed to produce food via targeted seed growth (Central Valley Joint Venture, 2006). Nevertheless, waterfowl rely upon anthropogenically regulated and limited agricultural food resources (rice and corn fields; Moyle et al., 2014; USBR, 2013), which the TRUEMET model estimates currently fulfill approximately 70% of their food needs (Central Valley Joint Venture, 2006). Problematically, increasing disturbance from growing urban populations or changing land management practices can unexpectedly transform advantageous food resources into crops of no value to waterfowl (e.g. nut orchards; Central Valley Joint Venture, 2006), diminishing suitability of agricultural resources (Eadie et al., 2008; Reijnen et al., 1995) and heightening the value of remaining food and sanctuary habitats.

Divergent movement and behavioral strategies detected with our high frequency data may be related to age/experience or species and could complicate population-scale environmental management. Ducks that have previously experienced a hunting season may be more familiar with the disturbance and become habituated sooner than novice individuals. This, combined with prior awareness of sanctuary locations, may enable them to adjust their behavioral responses more rapidly. While interspecific divergences are theoretically possible, all birds in this study were closely related dabbling ducks of the Anatidae family. These species predominantly use the same/similar habitats and perform comparatively similar movements (McDuie et al., 2019), which reduces the likelihood of divergent disturbance responses. Nevertheless, data from more individuals could help detect any influence of species and by tracking hatch-year birds, we could compare individuals undergoing their first hunting season and account for divergences among age cohorts.

Landscape level approaches to habitat management across multiple scales that are directly relevant to specific populations are often recommended for avian species (Stephens et al., 2004). For example, because habitat distribution directly influences duck movements (Casazza et al., 2012; Coates et al., 2012) and California ducks do not move very far on a day-to-day basis (McDuie et al., 2019), if sanctuaries do not provide the necessary resources or managed feeding habitats are too far from sanctuaries, the utility of both may be limited. Redirecting management resources that focus on providing food, into reconfiguring essential wetland habitats and distributing more sanctuaries across the landscape, would minimize distances between sanctuary and foraging areas and accommodate ducks' propensity for small movements. Additionally, augmenting suitable waterfowl habitat and improving access to currently avoided areas would alleviate negative effects of disturbance and unfavorable disease conditions caused by large concentrations of birds on wetlands (Davis et al., 1971; Wobeser, 2012). While dabbling ducks can rely predominantly on managed wetlands for their habitat needs (Casazza et al., 2021), the optimization of sanctuary and feeding areas within a habitat mosaic can better distribute and retain populations by promoting use of larger tracts of the wetland landscape and underpin a more robust ecosystem.

Our research shows that ducks are dramatically impacted by anthropogenic disturbance in numerous ways and they adjust to disturbance relatively quickly with substantial behavioral modifications that likely detrimentally affect their ability to procure sufficient food resources. Although a relatively small sample size, our marked ducks are sentinels for much larger aggregations due to their social, flocking nature. The highest disturbance generally caused ducks to remain in sanctuaries and forego daytime foraging, but they also amended movement patterns to avoid the more moderate disturbance of humans moving about the wetland landscape by foot or boat, both of which had the effect of increased nocturnal movement/foraging. Persistent modification of natural movement patterns impacts species ecology producing physiological, behavioral, management and conservation implications especially in highly modified systems such as California where historic habitat loss has corresponded with significant population declines (Frayer et al., 1989; Moyle et al., 2014). Wetland management is costly, so effective, efficient habitat development and enhancement is an important concern for land managers whose objective is to maximize carrying capacity and protect waterfowl populations (Central Valley Joint Venture, 2006; Smith et al., 1989). Future research is needed that focuses on determining the optimal size and juxtaposition of sanctuaries and food resources to better distribute essential habitats across the landscape and accommodate population needs. Our findings offer insights into improving environmental resource management for Pacific Flyway waterfowl and serve as an example to other systems impacted by anthropogenic disturbance where inhabitants respond by adjusting behavior. This new understanding of species ecology and improved knowledge of movement and behavior can inform the development of broadscale management and conservation approaches that will protect populations, keep these common species common (Gaston, 2010), improve biodiversity, and ensure healthy, functioning ecosystems.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2021.113170.

Credit author statement

Michael Casazza, Josh Ackerman and Cliff Feldheim conceived the broader research plan, and provide permissions and equipment. Fiona McDuie conceived the original idea, design and experiment and authored the manuscript. Cory Overton managed the larger database. All authors read and approved the final version for submission. Analyses were conducted by Austen Lorenz, Robert Klinger and Fiona McDuie. Austen Lorenz completed figures and mapping.

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