Tidally-Induced Limits to California Clapper Rail Ecology in San Francisco Bay Salt Marshes

By

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ABSTRACT

The state and federally endangered California clapper rail (*Rallus longirostris obsoletus*) has declined in abundance and been reduced in range and now occupies fragmented intertidal saltmarsh only within San Francisco Bay. Historically extensive salt marsh habitats existed in San Francisco Bay and today, remnants are largely restricted to the water's edge with dikes and levees separating marshland from modified habitats unsuitable for clapper rails. Clapper rail population abundance has roughly tracked a series of positive and negative impacts including market hunting at the turn of the 20th century, widespread habitat reduction and fragmentation, and invasive species introduction and eradication programs. Despite these changes, rail populations have been subject to the ebb and flow of the tides, which regularly inundate salt marsh habitats. The influence that tides have on vertebrate species living in intertidal saltmarsh should be substantial, but the relationship between tide and California clapper rails is poorly understood. This research identified important ways in which tides influenced demographic processes, space use, and resource selection in California clapper rails.

Tidal inundation in San Francisco Bay saltmarshes creates zonation in plant communities, typically with tall monocots in the low marsh (*Spartina* sp.), short pickleweed (*Sarcocornia pacifica*) in mid-elevation ranges, and gumplant (*Grindela humilis*) in the high marsh. Invasive Spartina (*Spartina foliosa x alterniflora*) grows taller and thicker than native Pacific cordgrass (*Spartina foliosa*). Invasive Spartina also grows lower onto mudflats, further up into pickleweed areas, and provided both nesting habitat and tidal refuge for clapper rails. In Chapter 1, I examined survival rates of California clapper rails. Specifically, I investigated whether seasonal patterns observed in the early 1990s were still evident and assessed the influence that Invasive Spartina and the degree of tidal inundation on weekly survival rates in four South San Francisco Bay salt marshes. Between January 2007 and March 2010, California clapper rail annual survival was 73% greater in Spartina-dominated marshes ($\hat{S} = 0.482$) than in a control marsh dominated by native vegetation ($\hat{S} = 0.278$). Lower survival also occurred during periods when tide height was greatest and during the winter. Survival patterns were consistent with Invasive Spartina providing increased refuge cover from predators during tidal extremes which flood native vegetation, particularly during the winter when the vegetation senesces.

Tide heights also strongly influenced selection for artificial habitats provided adjacent to one marsh during the winters of 2010-2011 and 2011-2012. Ten floating islands equipped with canopies providing cover were monitored using time-lapse cameras for evidence of clapper rail use. Clapper rails regularly used artificial islands once tides reached heights equal to the average surface elevation of the marsh. When tides had inundated the marsh plan, observed use of the artificial islands was more than 300 times expected use based on the surface area provided. Probability of use varied among the islands and low levels of use were observed at night. Endemic saltmarsh species are increasingly at risk from habitat change resulting from sea-level rise and development of adjacent uplands. Escape cover during tidal inundation may therefore need to be supplemented if species are to survive.

I developed a new method to estimate space use accounting for individual movement phases within non-stationary relocation datasets using simulated radio-telemetry data. To define movement phases I used a nonparametric, multivariate test to detect change points in the mean or variance of a sequence of x,y coordinates. Once all phases (change points) were identified, Gaussian kernel density analysis was used to estimate space use during each phase, which I termed change-point utilization distributions (CPUDs). One advantage of this technique is that the location of change points can subsequently be tested for relationships with conditions that might trigger a change in how individuals use space. Change points in clapper rail movement were associated with a variety of environmental and biotic variables including high tides, nesting activity, intrusion by neighboring clapper rails, and transient

movements outside the home range. Change points occurred more than twice as frequently during the highest observed tides relative to all other tide heights.

Another use of CPUDs is that space use patterns of adjacent individuals can be evaluated for joint overlap only during specific time periods when overlap occurs. I used CPUDs developed for California clapper rails and identified the point within overlapping space-use estimates where each individual had priority access to the resources within its utilization distribution (i.e. the lowest kernel density isopleth that was common to two overlapping individuals). This provided an estimate of the spatial region at which individuals exhibited territoriality. During the breeding season, space use distributions overlapped less and average territory size increased relative to the non-breeding seasons. Population density implied by these territory sizes (1.38 birds/ha) is comparable to density estimates during the 1970s and 1980s.

Together these findings show the great degree to which clapper rail behavior and demography can be influenced by the tides that populations experience. It is my hope that conservation efforts for this species, particularly in the arena of habitat restoration may benefit from this research.

This dissertation is dedicated to my grandparents, Elwood Stewart Overton (1926-2009) and Terril Arlene Overton (1931-2013), two of my first teachers who taught me the most important lessons that a young man could learn.

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"If we knew what we were doing, it would not be called research, would it?" – Albert Einstein

This work must truly have been research then since I did not know what I was doing most of the time, even as I was doing it. Fortunately, I had so much amazing support from so many people that I could not help but succeed in spite of myself. Chief among the reasons that this dissertation was finished at all was the guidance of my committee and principle investigators: Marcel Holyoak, Don Strong, John Eadie, Michael Casazza, and John Takekawa. I am not quite sure how they managed to keep me focused while simultaneously challenging me to expand my thinking and giving me free reign even when I was being difficult. I am well aware that I had a unique opportunity to thrive while in school due to their actions and support and I am deeply grateful that they found such a productive balance between pushing me forward and giving me room to breathe.

This work is the product of a community of people who make it their business and passion to better the world. I want to recognize the staffs of the Invasive Spartina Project, California State Coastal Conservancy, Point Blue Conservation Science, East Bay Regional Parks District, California Department of Fish and Wildlife, and US Fish and Wildlife Service who strive every day to make the marshlands of San Francisco Bay more complete and healthy. I want to give special recognition to Toby Rohmer. We started research together on clapper rails nearly 8 years ago now. He has been an amazing champion for making a healthier Bay ecosystem. Without his pioneering work, input, and hours-long late night conversations, I would never have been able to make it this far. I owe him more than he knows and I am thankful to call him my friend.

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Most of all, my deepest gratitude is for my family. My wife, Sawsan, who hasn't yet known me as anyone other than that crazy bird guy who tracks mud into the house at all hours of the day and night (Sorry dear, that probably won't change), is my own refuge when I get inundated. And my parents, who finally get to enjoy retirement and children who are no longer in school.

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INTRODUCTION

" 'They used to be common as them little marsh chippies,' said he, 'They'd nest wherever there was a little high ground, and sometimes on floating tule stems and such stuff. They used to nest right here by my house in Alameda…And now?' said the old hunter derisively repeating my question, '*Now*, they're all gone. I guess if you were offered a thousand dollars apiece for Rail out here you wouldn't get rich.'" – "Old Hunter" speaking to H. R. Taylor of California clapper rail (1894).

The plight of the California clapper rail (*Rallus longirostris obsoletus*) is a story that now spans three centuries. As early as the close of the 19th century there was recognition that populations, of this the largest and most colorful of the clapper rail subspecies, had declined precipitously (Taylor 1894). Clapper rails and their eggs were served in restaurants and populations were hunted to near extinction prior to establishment of the 1913 Federal Migratory Bird Law, to which the acclaimed naturalist Joseph Grinnell remarked that it provided "proof that adequate protection long enough continued will restore the species" (Grinnell et al. 1918). Unfortunately, Grinnell's predictions of more bountiful times ahead for the clapper rail were not to come to pass and the species has been protected at the inception of all major conservation legislation including the federal Endangered Species Protection Act of 1966 and Endangered Species Act of 1973 and the California Endangered Species Act of 1984 (USFWS 2010). By the time California clapper rails were afforded more formal protections, habitat loss due to anthropogenic conversion had replaced hunting as the primary cause for endangerment (USFWS 2010). This research project arose from contemporary questions regarding invasive species in clapper rail inhabited saltmarsh. It quickly became clear that regular tidal inundation made life in San Francisco Bay saltmarsh particularly dynamic.

It would be an overstatement to say that tides influence everything in a San Francisco Bay saltmarsh. However, for a terrestrial vertebrate like the California clapper rail, which is limited to intertidal habitats as well as prey for numerous avian and mammalian predators, the influence that tides had on rail behavior and habitats was both ubiquitous and predictable. With such an immutable force as tides that seemingly governed many aspects of clapper rail ecology, it quickly became apparent to me that effective management of this species and its habitats would require an understanding of how tides affect individual behavior and population dynamics. It is my hope that this research will guide habitat restoration plans currently being developed and increase awareness of how projected future sea levels may increase the risk of California clapper rail extinction.

Project Overview

The California clapper rail is the largest of the clapper rail subspecies. Males in this study weighed approximately 425 grams and females 325 grams. Both annual and seasonal home ranges used by clapper rails are small (3.1 ha and 1.5 ha, respectively; Rohmer 2010). The clapper rail is prey to a variety of raptors and mammalian predators and predation was the primary cause of mortality during this study. Population survival rates estimated during previous research suggest low annual survival rates with particularly low rates during the winter (Albertson 1995). Clapper rails lay large clutches (7-10 eggs) during a prolonged nesting season (March-August) and may double clutch as well as build "dummy" nests (Eddleman and Conway 1998). Both members of the pair incubate nests built of marsh vegetation that are built within stands of the dominant saltmarsh species in San Francisco Bay: cordgrass

(*Spartina* sp.), gumplant (*Grindelia* sp.) or perennial pickleweed (*Sarcocornia pacifica*). A pair will advertise territories using a variety of calls and vigorously defend territories during the breeding season (Zembal et al. 1989). Territoriality does occur outside of breeding activity as well, but apparently with lower intensity, particularly during extreme high tides when multiple individuals may occupy stands of tall vegetation or high ground that remains unflooded.

Urban development and conversion to agriculture and salt production have removed over 90% of the salt marsh that once existed in San Francisco Bay (Josselyn 1983). The period when saltmarsh conversion in San Francisco Bay was the greatest was concurrent with the initial concerns regarding California clapper rail populations, circa 1850-1910. However, rapid development of saltmarshes continued particularly during and after WWII (Josselyn 1983). The remaining saltmarsh in San Francisco Bay, though often fragmented (Evens and Collins 1992), comprises 77% of California's total stock of this critical habitat (Takekawa et al. 2013). These remaining fragments also exist largely on the bayward periphery of their historic extents (Josselyn 1983). Urban encroachment from adjacent upland areas has forced saltmarsh species such as the clapper rail into an ever-closer association with the Bay and the tides that are a part of it.

Conversion, loss, and fragmentation are not the only effects that have influenced California clapper rail habitats in San Francisco Bay. In the 1970's, restoration along Old Alameda Creek in South San Francisco Bay included Smooth Cordgrass (*Spartina alterniflora*) transplanted from the Atlantic Coast. The non-native plant rapidly hybridized with native Pacific Cordgrass (*Spartina foliosa*) and created a self-fertilizing hybrid, Invasive Spartina (*Spartina foliosa x alterniflora*), which spread throughout South San Francisco Bay prior to establishment of an eradication plan in 2005 (Invasive Spartina Project 2003). California clapper rail seek refuge and nest within stands of Invasive Spartina which grow taller, more densely, and across a greater elevation gradient than the native parents (Callaway and Josselyn 1992, Daehler and Strong 1996).

It is perhaps not surprising then to reflect on how California clapper rail populations have mirrored the impacts to their habitats in San Francisco Bay. From populations hunted to feed patrons in San Francisco's restaurants at the turn of the 20th century, to a series of federal and state protections beginning in 1913 and continuing to the present day. Estimation of the size of California clapper rail populations is particularly difficult due to tall marsh vegetation and the secretive nature of rails. Nonetheless, population estimates in the 1970's when first listed under the Endangered Species Act were 4,200-6,000 (Gill 1979), though populations apparently declined through the 1980s until reaching their nadir in 1991 when a few hundred individuals were estimated (Albertson and Evens 2000). Coincident with the rapid expansion of the newly hybridized Invasive Spartina, rail populations rebounded to an average of 1,425 birds between 2005 and 2008 (Liu et al. 2009), though populations have been reduced subsequent to Invasive Spartina eradication (McBroom 2012).

Study Area and Research Methods

This research took place in four South San Francisco Bay marshes selected due to high clapper rail numbers and various degrees of infestation by Invasive Spartina. In 2007, 10 clapper rails were captured and radio-marked using backpack mounted VHF transmitters in each of three marshes: Colma Creek Marsh, Cogswell Marsh, and Laumeister Marsh. Arrowhead Marsh was added in 2008 and each winter new birds were captured, or existing birds recaptured, to maintain a sample of approximately 10 birds in each marsh. Birds were tracked from the ground using handheld 3 or 4 element Yagi antennas and triangulated using 3 to 5 bearings to improve location estimates. Tracking to obtain location estimates also provided information for survival analyses (Chapter 1) due to the presence of a 4-hour mortality sensor included with each transmitter that signaled after prolonged immobility. Location estimates were used to identify changes in the movement process, and resulting territoriality, that individual birds exhibited (Chapters 3 and 4). During the winters of 2010-11 and 2011-12, floating artificial habitats that provided refuge during periods of tidal inundation were placed adjacent to Arrowhead Marsh. Use of these habitats by clapper rails and other species was monitored via time elapsed and motion sensing cameras. Tidal data obtained through a network of tide stations operated by the National Oceanic and Atmospheric Administration (NOAA 2011) allowed me to investigate how various tide heights influenced survival, movement patterns, and habitat selection of California clapper rails.

Chapter Summaries

Chapter 1 investigates seasonal patterns in California clapper rail survival rates and quantifies the effects of tide height and presence of Invasive Spartina on survival. In Chapter 2, I assessed California clapper rail use of artificial high tide refugia provided during two winters. These artificial habitats floated and provided constant habitat quality and quantity throughout the tidal cycle. In Chapter 3, I describe a new method to identify changes in the point patterns represented by radio-telemetry relocations using non-parametric and multivariate change point detection. I evaluated change points that occurred during the tracking period of radio-marked Clapper rails for potential triggering events such as extreme tides, nest initiation or cessation, and displacement by neighboring individuals. Lastly, in Chapter 4, I quantify the degree of territoriality displayed by adjacent pairs of clapper rails and resultant territory size. I then extrapolate these territory size estimates to population density estimates and compare these with previous research.

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CHAPTER 1: An invasive foundation species alters tidal habitat dynamics and increases survival of the endangered California clapper rail.

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ABSTRACT

Invasive species frequently degrade habitats, disturb ecosystem processes, and can increase the likelihood of extinction of imperiled populations. However, novel or enhanced functions provided by invading species may reduce the impact of processes that limit populations. It is important to recognize how invasive species benefit endangered species to determine overall effects on sensitive ecosystems. For example, since the 1990s, hybrid *Spartina* (*Spartina foliosa* x *alterniflora*) has expanded throughout South San Francisco Bay, USA, supplanting native vegetation and invading mudflats. The endangered California clapper rail (*Rallus longirostris obsoletus*) uses the tall, dense hybrid *Spartina* for cover and nesting, but the effects of hybrid *Spartina* on clapper rail survival was unknown. We estimated survival rates of 108 radio-marked California clapper rails in South San Francisco Bay from January 2007 to March 2010, a period of extensive hybrid *Spartina* eradication, with Kaplan-Meier product limit estimators. Clapper rail survival was 73% higher in hybrid Spartina dominated marshes before eradication ($\hat{S} = 0.482$) compared to both post-treatment marshes and a control marsh dominated by native vegetation ($\hat{S} = 0.278$). Lower survival occurred during the winter and during periods of high tidal inundation. Survival patterns were consistent with hybrid *Spartina* providing increased refuge cover from predators during tidal extremes which flood native vegetation, particularly during the winter when the vegetation senesces. Conservation actions to aid in recovery of this endangered species should

recognize the importance of available of high tide refugia, particularly in light of invasive species eradication programs and projections of future sea-level rise.

INTRODUCTION

Invasive species eradication is often undertaken to restore ecosystem health or improve function. Invasive species directly and indirectly affect native populations and communities (Crooks 2002; Vitousek et al. 1997; Vitousek 1990). Direct effects include altered resource availability, chemical composition, and physical structure, and indirect effects include modification of food webs, species interactions, and disturbance regimes. In addition, invasions often coincide with habitat degradation or altered climate condition causing complex interactions with ecological communities (Didham et al. 2007; Marvier et al. 2004). However, effects of invasive species are not all negative, and the "native good, alien bad" philosophy has recently been questioned (Goodenough 2010). Mechanisms by which native species can benefit from non-natives involve habitat modification, trophic subsidy, pollination, competitive release, predator release, and indirect effects resulting from predator-prey interactions or trophic cascades, potentially incorporating multiple invasive species (Bergstrom et al. 2009; Rodriguez 2006; White et al. 2006). In these situations, eradication may lead to insufficient "natural" habitat for native populations or the severing of biotic relationships that developed with invading species. Facilitation of native biota may also occur when the invasive species provides a limiting resource, functionally replaces a native species, or ameliorates depredation (Goodenough 2010, Rodriguez 2006). Facilitation by invasive species is increasingly recognized; for example, southwestern willow flycatcher (*Empidonax traillii extimus*) use tamarisk (*Tamarix* spp.) for nesting and migration stopover habitat where alternative habitat does not exist (Paxton et al. 2007). Facilitative interactions appear particularly important in stressful environments (Stachowicz 2001), and invasive species can ameliorate harsh environmental effects on other species, particularly when invasive species create novel habitats through ecosystem engineering (Rodriguez 2006; Watling et al. 2011).

Cordgrasses (*Spartina* spp.) are invasive ecosystem engineers that have invaded, hybridized (with related species), or created new invasive species through chromosome doubling (i.e. *Spartina anglica*), thereby invading saltmarshes in all continents (Ayres et al. 1999; Callaway and Josselyn 1992; Chambers et al. 1999; He et al. 2011; Strong and Ayres In Press; Zedler and Kercher 2004). Smooth cordgrass (*Spartina alterniflora*) invaded San Francisco Bay through restoration activities in 1973 (Faber 2000). For over a decade, the plant went virtually unnoticed until it hybridized with the native Pacific cordgrass (*Spartina foliosa*) and rapidly expanded throughout South San Francisco Bay (Ayres et al. 2004), eventually reaching northward to portions of San Pablo Bay. Native vegetation in San Francisco Bay saltmarsh conforms to strongly defined vegetation zones with *S. foliosa* at the lowest elevations, *Sarcocornia virginica* in the mid marsh, and a complex of high marsh vegetation including *Grindelia humilis, Distichilis spicata, Jaumea carnosa*, and *Frankenia grandifolia* in high or well-drained portions (Greenberg and Maldonado 2006; Hopkins and Parker 1984). Influx of freshwater in the northern reaches of San Francisco Bay allows various *Schoenoplectus* spp. and *Juncus* spp. to grow and creates qualitatively different vegetation conditions between the South and North Bays (C. Overton, personal observation). Hybrid *Spartina* grew in a similar manner to the tall-form of *S. alterniflora* on the Atlantic coast, where it forms dense monotypic meadows in the low to mid marsh and is outcompeted by *Spartina patens* in the highest tidal reaches (Bertness 1991). However, hybrid *Spartina* (*Spartina foliosa* x *alterniflora*) grows both lower and higher on the marsh plain than either parent species. Compared to *S. foliosa*, hybrid *Spartina* is also taller, grows more densely, and leaves greater residual biomass during the winter, resulting in more sediment accretion (Callaway and Josselyn 1992; Daehler and Strong 1996; Rosso et al. 2006). Hybrid *Spartina* developed several traits not usually seen in either parent species including: self-compatibility, rapid vegetative expansion, higher seed set than *S. foliosa*, and an Allee effect of faster than exponential growth in established clones (Ayres et al. 2008; Daehler and Strong 1997; Sloop et al. 2009). These traits, along with hybrid *Spartina*'s preadaptation to conditions, autogamic reproduction, vegetative reproduction, and phenotypic plasticity, match characteristics of other highly invading species (Baker 1965; Richardson and Pyšek 2006). Fear of increased flood risk, irreversible changes to tidal marsh geomorphology, and altered habitat structure affecting many sensitive species prompted planning for a large-scale eradication effort using herbicide and manual removal treatments by 2003 (Ayres et al. 2008).

The San Francisco Bay estuary also contains the last occupied habitat of the saltmarsh obligate California clapper rail (*Rallus longirostris obsoletus*; Takekawa et al. 2011); one of eight clapper rail subspecies in the U.S. and one of three Pacific coast subspecies each of which are threatened or endangered (Eddleman and Conway 1998). Historically, the California clapper rail ranged among intertidal saltmarshes along the California coast from Morro Bay to Humboldt Bay. With the exception of periodic sightings along the outer coast, current populations only occupy the highly fragmented remnant and restored marshlands in San Francisco and Suisun Bays. California clapper rails typically breed and forage in mid and lower intertidal vegetation communities, including in hybrid *Spartina*. They vigorously defend small seasonal (2 ha) and annual (4 ha) home ranges but will forage and seek refuge during tidal inundation higher in marshes, within taller vegetation, and along levee faces where sufficient cover and channelization exists (Eddleman and Conway 1998; Garcia 1995; Rohmer 2010). However, when suitable refugia are not available, clapper rails will occupy any available substrate (e.g. floating objects) even if it does not provide any cover (Cogswell 1977). Habitat conversion to agriculture, salt production, and development was the primary reason for both population declines and endangerment during the last century (U.S. Fish and Wildlife Service 2010). Native, synanthropic, and non-native avian and mammalian species depredate California clapper rails. Non-native red fox (*Vulpes vulpes*) were the suggested cause of population declines during the 1980s and early 1990s (Foin et al. 1997; Harding et al. 2001). Contemporaneous research suggested low annual survival rates compared to other clapper rail subspecies (Albertson 1995). Predator management and tidal marsh restoration were credited with apparent population recovery from a few hundred individuals in the early 1990s to 1,040-1,264 by the late 1990s (Albertson and Evens 2000). However, expansion of hybrid *Spartina* also occurred during this period of clapper rail recovery, which peaked in 2007.

Vegetation structure is often more critical than species composition for vertebrates. This is especially true in saltmarsh where processes governing population dynamics (e.g., survival, reproduction, and distribution) may be tidally driven. Lack of suitable escape cover during periods of tidal inundation may lead to increased depredation (Dekker and Ydenberg 2004). Reproductive trade-offs between the risks of flooding and risks of predation exist for many species of tidal wetland birds including non-threatened populations of clapper rails (Burger 1985; Eddleman and Conway 1998; Frederick 1987; Frederick and Collopy 1989; Gaines et al. 2003; Meanley 1985; van de Pol et al. 2010). Both saltmarsh sharp-tailed (*Ammodramus caudacutus*) and seaside sparrows (*A. maritimus*) nest in taller than average vegetation which is important for success of Seaside Sparrow nests (Bayard and Elphick 2011; Gjerdrum et al. 2005). Tidal influences may extend beyond the nesting period as well. Louisiana clapper rails (*Rallus longirostris saturatus*) avoid the edges of marshes, particularly during the first few weeks after nesting (Rush et al. 2010). During tidal inundation of marshes, raptor hunting success increased and avian prey species modified their behavior and habitat selection (Dekker and Ydenberg 2004; Rosa et al. 2006; Whitfield 2003). California clapper rail space-use patterns show strong clustering during both high and low tide periods and low rates of emigration to escape high floodwaters (Casazza et al. 2008; USGS unpublished data). Plant structure may indirectly facilitate persistence through provision of cover and nesting substrate during periods of tidal inundation when alternative vegetation is not of sufficient height to enable use across tidal inundation periods. The phenotypic differences of hybrid *Spartina*, compared to traits of native vegetation in San Francisco Bay, are consistent with increased provision of refuge cover for California clapper rails during periods of inundation.

Herbicide spraying to eradicate hybrid *Spartina* throughout San Francisco Bay began in 2005. Treatments included aerial, boat, vehicle, and backpack application of imazapyr (a non-selective, imidazolinone class, protein synthesis disruptor) to kill plants or conduct “chemical mow” treatments using reduced herbicide concentrations to prevent plant seed set and vegetative expansion (Invasive Spartina Project 2003). Despite the need for successive treatments to achieve complete removal, the effectiveness of the eradication program at removing *Spartina* in a single treatment was high (McBroom 2012). Prior to herbicide application, habitats used by radio-marked clapper rail in invaded marshes were taller than native marshes (USGS unpublished data). After two years of application, hybrid *Spartina* was shorter or absent from locations while native vegetation regrew and maximum vegetation heights did not differ between treated and native vegetation marshes (USGS, unpublished data). Coincident with hybrid *Spartina* control, population monitoring of California clapper rails indicated large declines in abundance (Liu et al. 2009; McBroom 2012).

In this paper, we examined how habitat dynamics created by vegetation phenology and hybrid *Spartina* eradication efforts affected California clapper rails survival in relation to various levels of flooding. Two of the main factors influencing vegetation during our study were seasonal plant senescence during the winter and application of herbicide. We hypothesized that the amount of tidal refugia provided by vegetation would decrease through the winter and used repeated measurement of vegetation height at fixed locations to test this hypothesis. We also evaluated change in refuge cover before and after herbicide application using remotely sensed data depicting vegetation heights. Lastly, clapper rail survival rates vary seasonally with the lowest survival rates during the winter (Albertson 1995). We hypothesized that tide levels and vegetation structure are responsible for this pattern. Therefore, we tested for effects of season of the year, tidal inundation, and hybrid *Spartina* on California clapper rail survival rates.

METHODS

Study Area and Telemetry Techniques

We captured and radio-marked California clapper rails with very-high-frequency (VHF) transmitters at four saltmarshes (Arrowhead [10 ha], Colma [25 ha], Cogswell [60 ha], Laumeister [36 ha]) in the southern reach of San Francisco Bay (Figure 1) between 2007 and 2009. Arrowhead was created by sediment deposited after the Lake Chabot Dam failed in 1874. Cogswell was previously diked and used for salt production and restored to tidal marsh in 1980. Laumeister has been saltmarsh for over 110 years, making it one of the oldest remaining marshes in the South Bay. Colma has been highly modified since the 1950s. Historically, much of the current marsh was mudflat with limited vegetation that consisted mostly of *S. foliosa* and *S. virginica*. By the mid-1980s, hybrid *Spartina* had heavily invaded Colma and expanded throughout the marsh into adjacent mudflats. Arrowhead Marsh was included in capture efforts beginning in the winter of 2008. Selection of marshes was limited by logistical and legal constraints. Populations of clapper rails needed to be sufficiently large to allow radio-marking without unduly risking viability of entire subpopulations. Additionally, hybrid *Spartina* eradication was being conducted at all known locations of invasion, and thus, randomized application of treatments was not possible. We contrasted estimates of survival between three groups: marshes prior to hybrid *Spartina* eradication efforts (Before), after efforts were initiated (After), and marshes with no hybrid *Spartina* to be treated (Control).

Capture and radio-marking occurred from December to March at all sites, and we employed two methods depending on the geomorphology of each marsh. We used drop-door traps modified with fishing line tripwires and placed in tidal channels to catch rails during lower tides and Cogswell and Laumeister marshes. At Colma and Arrowhead, we caught rails by hand and with dip nets during the highest tides of the tidal cycle. Rails were fitted with 9.5 g backpack transmitters (Model A1120, Advanced Telemetry Systems, Asanti, MN) attached using modified Dwyer harnesses (Dwyer 1972) made of Teflon™ ribbon (Bally Ribbon Mills, Bally, PA, USA). Rails were monitored intensively for the first two days after marking with repeated attempts at visually observing the bird to verify transmitter fit and acclimatization. We recaptured surviving birds and refitted them with new transmitters after 10-13 months (Table 1).

California clapper rails were relocated 1- to 10-times per week using handheld 3-element Yagi antennas from the perimeter of the marshes at distances 10-400 m from the bird. Transmitters included mortality switches designed to signal inactivity of more than 4 h in duration to enable rapid detection of mortalities. We identified proximate causes of clapper rail mortality based on the condition of remains and available ancillary evidence. Presence of plucked feather piles indicated raptor predation, while crushed bones and burying indicated mammalian predation. We sent samples with no obvious cause of mortality to the U.S. Geological Survey National Wildlife Health Center (Madison, Wisconsin, USA) for necropsy. We discovered most carcasses within 2 days of mortality and were confident that scavenging did not bias the assignment of causes of mortality. When radios failed, or emigrating individuals could not be relocated, ultimate fate could not be determined, and we right censored the individuals in the survival analysis (Kaplan and Meier 1958).

Analysis and Covariates

We estimated the seasonal dynamics of intertidal vegetation structure in 2010 and 2011 at 50 random locations in Arrowhead marsh. We recorded maximum vegetation height within 1 m of each random point 4 times between September 2010 and April 2011. Each random point was marked with a Real-Time Kinematic (RTK) global-positioning system (GPS) unit (Leica Geosystems, Norcross, GA) to record elevation (± 2 cm accuracy). We added vegetation height to ground elevation to identify the tallest cover with respect to tidal height. A Bayesian random slope and random intercept repeated-measures linear mixed regression model (LMM, WinBUGS) was used to quantify senescence patterns and change in the provision of refuge cover across all points (Gelman and Hill 2006). The random intercept was included for each of the 50 sample locations with a random slope allowing the rate of vegetation senescence to vary according to initial height. This allowed estimation of a linear relationship between refuge cover height and time without violating the necessary assumption of uncorrelated and normally distributed error structure that would be present in heteroscedastic data (Jacqmin-Gadda et al. 2007).

We assessed vegetation change resulting from hybrid *Spartina* eradication efforts using LiDAR data collected before and after herbicide treatments. We obtained LiDAR data through the Center for LiDAR Information Coordination and Knowledge (CLICK) website (http://lidar.cr.usgs.gov, Last Accessed March 24, 2012). Data on 2004 and 2010 habitat structure were available for each of our study marshes. The data available for 2004 were taken three years before the start of our radio-telemetry study when hybrid *Spartina* was near its maximum extent throughout San Francisco Bay (McBroom 2012). No major alterations to vegetation structure were evident in any of our study sites between the 2004 data acquisition and the start of our research except hybrid *Spartina* continued to expand during this period. Therefore, the 2004 LiDAR data provides a representation of the refuge cover condition in our marshes before treatments occurred. LiDAR data for 2004 were developed for the Federal Emergency Management Agency Flood Hazard Mapping Project or for the San Francisco Estuary Institute and U.S. Geological Survey (USGS) Center for Earth Resources Observation and Science. LiDAR data for 2010 were collected for the American Recovery and Reinvestment Act USGS San Francisco Coastal LiDAR Project. Surface elevation models were developed using ENVI software (Excelis Visual Information Solutions, Boulder, CO, USA). Elevation models were represented in 1-m square pixels using first return LiDAR data after mosaicking tiled datasets to the region of interest and filtering erroneous elevations. We used control points on unobstructed hard surfaces (e.g. roads, trails, flat building roofs) to verify vertical accuracy and consistency in estimated elevation for each LiDAR data set. Surface maps were then restricted to marsh boundaries plus a small buffer, approximately 5 m, representing both tidal flat foraging areas and potential upland-tidal marsh ecotone refuge areas. Tide conditions vary throughout San Francisco Bay so all elevations were rescaled to represent local inundation patterns. Rescaling was done according to the formula:

$$\text{Refuge potential} = \frac{(\text{Surface elevation - Mean Sea Level})}{(\text{Mean Higher High Water - Mean Sea Level})}$$

In the resulting scale, 0 represents mean sea level (MSL) and 1 represents MHHW. The advantage to rescaling elevation was that vegetation composition in intertidal saltmarsh has strong zonation with different species tolerating different degrees of inundation best represented over large geographic scales using relative elevations as opposed to absolute elevation (Hinde 1954; Swanson et al. 2013).

We employed the Program MARK “Known Fate” subroutine (White and Burnham 1999), which uses the Kaplan-Meier product limit estimator, and a logit-link, to estimate weekly survival rates (Kaplan and Meier 1958). We developed a weekly encounter history for each bird that indicated presence in the study area and incidence of death. Encounter histories were grouped by treatment type (Before, After, and Control). Individuals alive through the pre-eradication period were right censored in the Before treatment group at the start of the winter following the initial *Spartina* treatment and left censored in the After treatment group. One advantage of the Kaplan-Meier estimator lies in its ability to account for censored individuals using staggered entry (Pollock et al. 1989). We used time varying indicator variables to assess seasonal differences in survival. Three ecologically relevant seasons were investigated; Breeding (March 15 to July 14), Post-Breeding (July 15 to November 14) and Winter (November 15 to March 14). We chose the season names to represent the primary behavioral activities clapper rails exhibit during the periods. The period timeframe however represents the vegetation phenology occurring in the tidal marsh. The Breeding period occurs during spring green up and plant growth when plants are mostly below the maximum height attained in a year. The Post-Breeding period occurs when plants are at the maximum height and when flowering occurs. The Winter period is characterized by plant senescence and degradation by tides. We used time–varying continuous variables to estimate the effects of average and maximum weekly tide levels on survival. Individual covariates identifying capture site, sex, and time–varying indicator variables for year of study were included to test for potential confounding differences in survival. Random effects models can be used to account for temporal or spatial variation, but these effects were confounded with the primary effect and lacked sufficient levels to model their distributions properly (Burnham 2012). A full list of variables included and models considered are available online (Supplement 1).

We used Akaike Information Criterion (AICc) to determine the best-fitting models from those tested (Burnham and Anderson 1998). We contrasted group survival rates (Before versus After versus Control) after accounting for environmental and temporal variation. We refer to “competing models” within 2 AIC units of the best performing model for clarity. Potential confounding spatial or temporal variation were evaluated independently (relative to null) of the competing models to provide robust model-averaged parameter estimates (Burnham and Anderson 1998). Site–level variation was highly confounded with treatment group and caused estimation and convergence failures when the two variables were included together in models. Therefore, we did not attempt to model site variation in conjunction with Spartina treatment group. All interpretation our model results focused on model-averaged effect sizes (Burnham and Anderson 1998) and relative ranking of nested models (using AICc weights). We assessed effects of transmitter attachment on clapper rails through behavioral observation, changes in body condition, and comparison of survival rates between newly marked birds and birds that had shown resilience in carrying transmitters for a full year. Since age of individuals is not identifiable during the capture season, we could not assess this effect differentially between adults and hatch-year birds. We assumed that the resilience of individuals from the previous cohort year (previously marked birds) was the same as the following year (newly marked birds).

Captured rails were sexed based on morphology or genetic analysis of blood samples (Overton et al. 2009). We obtained tide heights from a National Oceanic and Atmospheric Administration (NOAA) continuous tide monitoring station centrally located near Redwood Creek. Weekly mean higher high water (MHHW) and maximum higher high water (MaxHHW) were calculated from verified online data (NOAA website http://tidesandcurrents/noaa.gov accessed August 2nd, 2010). Local tide patterns constrain marsh vegetation, elevation, and geomorphology (Hinde 1954; Redfield 1972); therefore, a single relative tide height (e.g. Redwood Creek) was more appropriate to assess tidal effects across sites than tide heights at individual marshes. The effect of high water on survival of rails was expected to be most pronounced during the winter when *Spartina* had senesced and been degraded by high tides. An interactive effect of tide height and season was therefore included in our statistical models. Herbicide application to eradicate hybrid *Spartina* occurred annually between August and October throughout the study. Methods of application included helicopter, vehicle-mounted, or backpack spraying using dyed herbicide to restrict application to hybrid *Spartina* only (Invasive Spartina Project 2003). This minimized effects of herbicide on native vegetation, which rapidly recolonized areas after *Spartina* removal (Hogle 2011). Laumeister was classified as the Control marsh because hybrid *Spartina* eradication was limited to a few isolated clones of <1 ha. Marshes in which hybrid *Spartina* initially occurred ("Before Eradication") were categorized as "After Eradication" during the winter following the first application of herbicide treatments (Table 1). Efforts to finish eradication of hybrid *Spartina* were still ongoing at all sites, but significant reduction in *Spartina* cover and biomass occurred in the first year following initial treatments (Hogle 2011, McBroom 2012). Prior to herbicide application invaded marshes had significantly taller vegetation than the native marsh. Following herbicide treatment, hybrid *Spartina* decreased in height while native vegetation, particularly *Sarcocornia virginica*, regrew (Hogle 2011). After two years of herbicide application, the maximum vegetation heights were not different between invaded and native marshes (USGS unpublished data).

RESULTS

We rejected the null hypothesis that availability of refuge habitat remained consistent throughout the winter. The maximum elevation of vegetation at Arrowhead Marsh declined by 4.3 cm in every bimonthly sampling period (95% credible interval=-6.2 to -2.3, n=200) resulting in an average total decline of 34.4 cm from September 2010 to April 2011. However, this decline was not uniform across the marsh since plants that represented the tallest vegetation and greatest refuge cover declined more rapidly than shorter and lower elevation plants (i.e. random slope and intercept effects were correlated, Figure 2). The proportion of vegetation providing adequate refugia for rails during winter tides remained consistent between September and November, and then declined rapidly in February and April (Figure 3).

Longer term habitat dynamics resulting from hybrid *Spartina* eradication efforts, as indicated by LiDAR derived digital elevation models, showed decreased availability of high tide refuge cover relative to conditions prior to eradication. LiDAR maps consistently estimated elevation of static surfaces (e.g. roads) between 2004 and 2010 with ranges from -7 cm to +8 cm for all marshes. This was lower than the 12 cm vertical root mean squared error (RMSEz) standard which was the maximum error for individual data sets assessed using ground control points and an Airborne Global Positioning System base station (Dewberry 2011a, 2011b; Foxgrover and Jaffe 2005). Thus, LiDAR change within the marshes between 2004 and 2010 indicated change in plant structure following *Spartina* eradication efforts and not inconsistency in estimated elevations. Surface elevations and the proportion of habitat above mean higher water declined for all three marshes where hybrid *Spartina* eradication occurred (Figure 4, Table 2). At Laumeister Marsh, where hybrid *Spartina* did not occur, surface elevations and proportion of habitat above MHHW increased very little between 2004 and 2010 (Figure 4, Table 2). Our results indicate a marked decline in refuge cover available for clapper rails in marshes following hybrid *Spartina* eradication efforts, despite recolonization by native vegetation (McBroom 2012; USGS unpublished data).

We captured and radio-marked 108 California clapper rails (Table 1) and estimated survival over 166 weeks. One hundred and six mortalities were caused by predation. The specific agent of mortality was confirmed for 70 clapper rails due to rapid recovery of carcasses, diagnostic evidence of remains and/or laboratory necropsy. Two rails died of disease, one from non-predation trauma, and the remainder from predation by raptors (30) or mammals (27). We found no evidence that transmitters caused lower initial survival rates following capture, changed physiology, or prevented breeding. Transmitter and capture effects should be identifiable through lower survival soon after marking, but over the same time period, newly marked birds had no detectable difference in survival than individuals marked the previous year (95% CL: -7.0% to +7.8%). Both males and females nested, including several pairs where both adults were radio-marked. Mass of individuals recaptured one year following marking on average dropped less than 1% from initial marking (n= 24; range -8.2% to +12.2%). Data were not available for an independent validation of survival rates and assessment of transmitter effects, but the data available indicate that capture and marking had little effect on survival and marking did not affect body condition or reproductive potential.

Four competing models contained variables accounting for seasonal differences in survival rates, MaxHHW, and differences in rates due to hybrid *Spartina* treatment (Table 3). Potential confounding spatial or temporal variation were evaluated independently (relative to null) with the four top–ranked models from the candidate model set to provide robust model-averaged parameter estimates (Burnham and Anderson 1998). Site–level variation was highly confounded with treatment group and caused estimation and convergence failures when the two variables were included together in models. Therefore, we did not attempt to model site variation in conjunction with *Spartina* treatment group. Covariates accounting for survival variation according to site, sex, or annual differences in survival rates all received little support from the data. The model-averaged survival rate was 0.978 (95% CI: 0.960-0.988) per week across all marshes, treatments, and years. These estimates yielded average annual survival rates across all marshes of 0.315 (95% CI: 0.120-0.541).

We evaluated three related hypotheses; specifically that survival of California clapper rails was not related to: 1) season, 2) tide level, and 3) *Spartina* eradication treatments. Our best-supported model contained all three of these effects, and models containing each effect individually outperformed the null hypothesis; therefore, we rejected all three of these additional null hypotheses. Seasonally varying survival was present in all competing models and was the most important effect in our models based on relative likelihood values for models containing that effect. Model-averaged weekly survival probability was lower in the winter season (Dec 16 – March 15; 0.963), with breeding (March 16 – July 15) and post-breeding season (July 16 – December 15) survival rates approximately equal (0.985 and 0.990, respectively). Seasonal risk of mortality (i.e. 1-$\hat{S}$) was more than twice as great in the winter than in other seasons.

Weekly MaxHHW was present in the top three models (ΔAICc < 2.0) but absent from the fourth model indicating potential multicollinearity with the season variable. This was a reasonable finding since tide ranges near the winter solstice are greater in San Francisco Bay than other seasons. However, models including the effect of maximum water level did explain more variation in survival rates, and we retained the effect even in models including seasonal effects. Weekly MaxHHW was negatively correlated with survival during all seasons. Seasonally varying tidal effects outperformed models allowing only a constant effect of tide level throughout the year; these models likely represent the influence of vegetation structure, which differed in each season. The effect of maximum tide level was greatest during the winter relative to equivalent tides during other seasons (Figure 5). Qualitatively similar patterns were estimated when weekly MaxHHW was modeled as an additive effect with seasonal survival differences. Contemporaneous seasonal vegetation structure data were not available to test their effect in models of survival.

The best performing model differentiated survival probability into the three treatment groups, and all models including this effect outperformed the null model (Figure 6). Model averaged weekly survival in marshes prior to initial efforts to eradicate hybrid *Spartina* (0.985; 95% CL: 0.973 to 0.992) was higher than after eradication efforts began (0.975; 95% CL: 0.960 to 0.985) and higher than at Laumeister Marsh (0.972; 95% CL: 0.947 to 0.985) which did not contain hybrid *Spartina*. The presence of untreated hybrid *Spartina* increased rail survival by nearly 70%. Extrapolated annual survival in marshes with hybrid *Spartina* prior to treatment was 0.466 (95% CL: 0.419 to 0.518) and was 0.275 (95%

CL: 0.235 to 0.321) after eradication began. Extrapolated annual survival was 0.227 (95% CL: 0.185 to 0.279) when only native vegetation was available to clapper rails. This effect size represented significantly higher survival with hybrid *Spartina* relative to survival after initial herbicide application (change in weekly survival of 0.00994; SE = 0.00634; p = 0.059). The relatively large differences in survival rates indicate a major increase in clapper rail survival when hybrid *Spartina* is present and dense in saltmarshes. We estimated greater differences in survival between hybrid *Spartina* dominated marshes (Before treatment) and survival in native vegetation (difference in weekly survival 0.0135; SE = 0.00751; p = 0.036), while no significant difference existed between treated and native marshes (difference in weekly survival 0.0034; SE 0.00864; p = 0.679). This may have reflected residual hybrid *Spartina* that often remained as shorter refuge cover in marshes during the first years following treatment (McBroom 2012; USGS unpublished data).

DISCUSSION

California clapper rail population trends mirrored invasion of South San Francisco Bay by hybrid *Spartina*. Increase in the clapper rail population abundance from a few hundred individuals to a few thousand individuals coincided with expansion of hybrid Spartina throughout South San Francisco Bay (Albertson and Evens 2000). Clapper rail populations have declined following efforts to eradicate hybrid *Spartina* (Liu et al. 2009). Furthermore, the highest clapper rail densities frequently occur in invaded areas. Altered survival is a likely mechanism that accounts for these patterns, and the highest survival rates we estimated occurred in marshes with substantial infestation by hybrid *Spartina*. Following herbicide application, these same marshes had survival rates equivalent to a marsh with native vegetation only. Survival of clapper rails decreased during periods of greater tidal inundation in all marshes, but the impact of tide level was greatest in the winter when vegetation senesced and reduced available refuge cover. In concordance with this seasonal pattern, Albertson (1995) also found similarly low survival rates during the winter in saltmarshes with native vegetation. We believe that it is differences in the vegetation structure provisioned by hybrid *Spartina*, rather than species composition *per se*, which facilitated higher clapper rail survival within invaded marshland.

Invasive species can ameliorate harsh environments by creating novel habitats through ecosystem engineering (Rodriguez 2006; Watling et al. 2011). This facilitation may be particularly important to mediate persistence in stressful environments (Stachowicz 2001). Extreme tidal inundation, though occupying a small portion of the year, dramatically alters the suitability of habitats to provide escape cover. Clapper rails use tall vegetation as refuge from predation, which becomes less available during tidal inundation and during the winter when vegetation senesces. We found that hybrid *Spartina* used by radio-marked California clapper rails in 2007 was taller than similarly used native marsh vegetation, but within two years after application of herbicide, the height of hybrid *Spartina* had dropped and native vegetation regrown sufficiently for no differences to have been evident between treated and untreated marshes (USGS unpublished data). The rapid return of native plant species following herbicide treatment (McBroom 2012) imply that within the highly fragmented and greatly altered marshlands in San Francisco Bay, hybrid *Spartina* provides higher quality tidal refugia and over a greater range of environmental conditions than native vegetation. This suggests that even with active restoration of saltmarsh vegetation, the eradication of hybrid *Spartina* will have negative consequences for California clapper rails. The impact on the endangered southwestern willow flycatcher of large-scale control efforts of tamarisk offers interesting parallels to the current hybrid *Spartina* effort. Willow flycatchers benefit from the structure provided by non-native tamarisk particularly where native riparian plant communities are absent (Sogge et al. 2013). Tamarisk was also the focus of a major removal effort involving biological control by the tamarisk leaf beetle (*Diorhabda* *oblongata*), which defoliates tamarisk during the summer coinciding with the flycatcher's breeding activities (Paxton et al. 2011). Concerns about the effect of defoliation during this critical reproductive period were compounded by uncertainty on the pace and ability of native riparian woodlands to replace tamarisk and led to cessation of biological control efforts by the US Department of Agriculture (Sogge et al. 2013). The potential impacts of hybrid *Spartina* removal on clapper rails have raised similar concerns.

Sea-level rise is a recognized concern that may influence clapper rail survival and suitability of already degraded habitats (U.S. Fish and Wildlife Service 2010). San Francisco Bay saltmarshes exhibit extreme spatial and seasonal variation in tidal cycles (Figure 1). During our study, mean tide range at the Golden Gate Bridge was 1.25 m, but this increased to 2.20 m at the extreme southern reach of our study area (National Oceanic and Atmospheric Administration 2011). The highest tides inundate large sections of marshland and constituent vegetation. Coupled with seasonal vegetation senescence patterns and damage from storm surges, the habitat available as refuge cover for saltmarsh obligate species is highly variable and becoming more limited as sea level increases (Flick et al. 2003; National Oceanic and Atmospheric Administration 2009). Even when fully mature, native vegetation would not be able to replace losses of the novel refuge cover provided by hybrid *Spartina* given the current state of San Francisco Bay marshlands. Sea level rise scenarios typically assess increases in mean sea level (Flick et al. 2003). However, some research suggests that tidal maxima (high and higher high water) are increasing faster than mean sea level and indicates limitation of tidal refuge may become more severe in the future (Cayan et al. 2008). *Spartina* species are known ecosystem engineers highly valued for maintaining shorelines, largely through increased sediment deposition (Strong and Ayres 2009). These effects may be delayed if sedimentation rates can offset sea level rise. However, under all scenarios, San Francisco Bay is expected to lose high marsh habitat that serves as refuge during extreme tides (Stralberg et al. 2011; Takekawa et al. 2013).

Our findings do not discount the potential for larger scale and extrinsic factors to influence clapper rail survival. California clapper rail populations declined substantially between 2007 and 2008; this pattern was also noted for the light-footed clapper rail (*R. l. levipes*) in southern California (Zembal et al. 2009). No specific process has been investigated that would cause such wide-scale regional synchrony in terrestrial population regulating mechanisms, but large-scale climate patterns are associated with changes in communities of marine species in San Francisco Bay and off the California coast (Cloern et al. 2010; Sydeman et al. 2013). Continued monitoring for population synchrony between these subspecies is warranted. Predator-prey relationships are also likely to play a role in regulating individual populations. Avian predator abundance in California increases markedly for some key species in the winter compared to other seasons (Wilkinson and Debban 1980). In particular, the short-eared owl (*Asio flammeus*) and peregrine falcon (*Falco peregrinus*) are known predators of clapper rails and both achieve their highest annual abundances during the winter. Most mammalian predator species do not migrate into saltmarsh habitats during the winter, but seasonal changes in diet, either behavioral (e.g. prey switching) or through additional opportunity provided by decreased vegetation cover, could result in increased depredation by generalist predators.

Density-dependent survival is a third mechanism that could explain seasonal survival differences. Rail populations reach their highest annual densities late in the breeding season. Lower winter survival could represent population regulation following fledging of young that are independent of adults at six weeks of age (Adams and Quay 1958). Survey methods that rely on indices of abundance from pre-breeding call counts may not accurately reflect changes in numbers of breeding individuals or represent post-breeding population abundance, particularly across variable habitat types (Anderson 2001; Conway et al. 1993). Regardless, we feel this explanation falls short since clapper rail density was generally declining during our study. If density-dependent survival was operating, survival should have increased when rail abundance declined, but there was no support for that pattern in our survival models.

IMPLICATIONS

California clapper rail populations have been declining for over 50 years (Albertson and Evens 2000; Liu et al. 2009). Our survival estimates represent the lowest known survival rates for any clapper rail subspecies and appear consistent with recent levels of decline. Current clapper rail management plans to reverse the population trajectory and recover the species focus mainly on protection and restoration of native saltmarsh habitats previously converted to for salt production (U.S. Fish and Wildlife Service 2010). Negative effects of hybrid *Spartina* in the tidal environment are well-documented (Daehler and Strong 1996; Grosholz et al. 2009) and threaten restoration activities. Eradication of hybrid *Spartina* is viewed as a prerequisite to prevent establishment of this invasive species in newly restored tidal marshes. However, there is increasing recognition that invasive species control may have unintended negative consequences for native bird communities, particularly where seasonal changes in vegetation structure affect demographic rates (Paxton et al. 2011). Recommendations for mitigating the negative effects of invasive species control have included maintaining existing un-invaded native habitats, restoring native vegetation, and balancing loss of non-native habitat that is lost with adjacent native habitat (Paxton et al. 2011). Our results suggest that high quality habitat for clapper rails should recognize both short term (3-5 h), and seasonal (3-4 mo) limitation in tidal refuge cover that reflects a bottleneck in annual survival rates.

The remaining natural habitats in San Francisco Bay may not currently provide high quality habitat for clapper rails, and nearly 96% may convert to mudflat under projected sea-level rise scenarios

(Cayan et al. 2008; Takekawa et al. 2013). Short vegetation, or that which occurs at the lowest elevations of the marsh, may provide suitable habitat 95% of the year but may be unsuitable during critical high tide periods. Since native vegetation does not attain the same biomass or height as hybrid *Spartina*, restoration with native species (e.g. *S. foliosa*) following hybrid *Spartina* eradication may still not provide sufficient tidal refugia for clapper rails to achieve the population sizes apparent in invaded marshes. Habitat modification that decreases available refuge during these critical periods should be considered when assessing effects on clapper rails. Long-term changes to the intertidal marsh ecosystem are ultimately responsible for populations that are not self-sustaining (Albertson and Evens 2000). Around 90% of marshlands in San Francisco Bay have been lost or converted to other land uses causing reduction and fragmentation of remaining marshlands (Goals Project 1999). Since larger marshes are more likely to have heterogeneous elevations, and given that most of the conversion for development occurs from the upland transition areas into the high elevation marsh, it is reasonable to assume that tidal refuge was disproportionally affected by past land use changes. Restoration actions, particularly conversion back to tidal saltmarsh, should seek to develop habitats that provide tidal refuge cover throughout the year by restoring heterogeneity in marsh elevations as well as native vegetation communities.

The effects on clapper rail survival and habitat suitability from sea-level rise are likely to vary between San Francisco Bay subregions. The tidal prism moving water in and out of San Francisco Bay determines high-tide level. The natural lateral constriction and shallow depth of South San Francisco Bay leads to a greater tidal range than in North San Francisco Bay marshes, which creates microhabitat conditions suitable for different plant communities in the two areas (Figure 1). These different plant communities may respond differently to increased inundation frequency and depth, unless vertical sediment accretion can keep pace. In most portions of San Francisco Bay, upslope migration of marshes is no longer possible due to levees, and failure to achieve suitable accretion is likely to result in changes in vegetation composition. Since native *S. foliosa* typically grows among the lowest elevations, replacement of high and mid-marsh vegetation by *S. foliosa* may occur with sea-level rise. *Spartina foliosa* is much taller than most species, which occur higher in San Francisco Bay intertidal marshlands. This could result in increased rail survival, particularly in breeding and post-breeding seasons if *S. foliosa* provides more tidal refugia than existing vegetation. However, this effect may be lost when *S. foliosa* senesces and degrades in the winter. Future conservation of California clapper rails will have to address the loss of novel ecosystem function that hybrid *Spartina* provided as refugia during tidal inundation.

We recommend additional research assessing the impacts of habitat structure and modification on recruitment of California clapper rails. Tide height may also affect the reproductive ecology of clapper rails (De Groot 1927; Harvey 1988; Kozicky and Schmidt 1949). Although prior research in San Francisco Bay indicated little nest failure due to inundation (Schwarzbach et al. 2006), this pattern may change as a result of habitat modification toward shorter vegetation species or with sea-level rise. The greater tidal range in South San Francisco Bay compared with North San Francisco Bay (Figure 1) is likely to make density independent (abiotic) population regulation through tide height and available cover a greater factor. Additional research is needed into alternatives to existing tidal refugia that facilitate survival rates equivalent those provisioned by hybrid *Spartina*, such as islands. Levees have replaced these natural features in most remaining San Francisco Bay marshlands while mammalian predators have proliferated in the highly urbanized landscape of San Francisco Bay (Foin et al. 1997; Lewis et al. 1999). Easily accessible terrestrial refugia may present rails with greater exposure to mammalian predators than flooded intertidal refugia, as seen in other waterbirds (Pierluissi 2010). Increased terrestrial refugia could result in increased predation rates, compared with intertidal refugia, if anthropogenically subsidized predators can gain easier access to clapper rails. Predator management for red fox coincided with expansion of hybrid Spartina in South San Francisco Bay and eradication of hybrid Spartina may change the effectiveness of predator control (Harding et al. 2001). We recommend that red fox control be reevaluated to determine if clapper rail populations have continued to respond positively following eradication of hybrid *Spartina*.

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TABLES

Table 1.1 Number of radio-marked California clapper rails present in four South San Francisco Bay salt marshes during the capture season, November-March, and used to estimate survival rates, January 2007-March 2010. Presence of invasive Spartina prior to eradication efforts is indicated by an asterisk. Arrowhead Marsh was not included in capture efforts until the winter of 2008-2009. Capture in the winter of 2010 occurred only at Arrowhead and Colma Marshes for subsequent studies.

Marsh	2007	2008	2009	2010
Arrowhead		10*	14	10
Cogswell	11*	9*	13*	2
Colma	9*	16	14	9
Laumeister	10	16	5	1

Table 1.2 Known-fate model results from Program MARK version 5.1 run on 108 California clapper rails radio marked in South San Francisco Bay January 2007 through March 2010. Only competing models (Delta AICc <2.0), global, and null models are presented. All models incorporating average weekly higher high water, annual, site or sex specific survival rates were poorly supported (AICc weight <0.03, Model Likelihood <0.1). A full explanation of variables used and candidate model set is available online (Supplement 1).

Model Rank	**Model**	**Delta AICc**	**AICc weight**	**Model Likelihood**	**# of Parameters**	**$LR^{2\ a}$**
1	Constant survival + Seasonal MaxHHW + Treatment Group	0.0000	0.2304	1.0000	6	0.2420
2	Constant survival + Seasonal MaxHHW	0.3727	0.1912	0.8300	4	0.2105
3	Seasonal survival + MaxHHW	1.0325	0.1375	0.5967	4	0.2057
4	Seasonal survival	1.9638	0.0863	0.3746	3	0.1837
17	Constant survival (Null model)	19.8424	0.0000	0.0000	1	N/A
26	Week specific survival (Global model)	177.261	0.0000	0.0000	166	0.9238

[a] = Likelihood pseudo-R^2 calculated using the method of Nagelkerke (1991)

$R^2 = (1 - (L(\text{intercept model [17]}) / L(\text{full model}))^{2/N})/(1 - (L(\text{intercept model [17]})))$; where L() is the likelihood of the model and N = number of samples [N=108].

Table 1.3 Tidal characteristics and high tide refuge habitat at four salt marshes in South San Francisco Bay. Habitat characteristics determined by LiDAR first-return surface elevation maps and represent minimum elevation of habitats in 2004 and in 2010.

Marsh	**Size (ha)**	**MSL**	**MHHW**	**Tide Rise**	**Proportion of Marsh above MHHW 2004**	**Proportion of Marsh above MHHW 2010**
Arrowhead	19.1	1.09	2.03	0.94	2.6%	0.6%
Colma	32.2	1.15	2.14	0.99	12.8%	9.3%
Cogswell	78.2 [a]	1.16	2.28	1.12	13.5%	5.5%
Laumeister	39.2	1.24	2.31	1.07	50.5%	77.7%

[a] =Cogswell Marsh is 84.8 hectares but due to gaps in the flightline of LiDAR data only 78.2 hectares were assessed.

FIGURES

Fig. 1.1 Survival rates of California clapper rails were estimated during 2007-2010 from 108 radio-marked individuals at 4 tidal saltmarshes in South San Francisco Bay. Tide range varies throughout San Francisco Bay with greatest amplitude in the South Bay. Verified tide data used in analysis from NOAA Tide and Currents webpage was obtained at the Redwood Creek tide gauge (http://www.tidesandcurrents.gov; Accessed May 11, 2011)

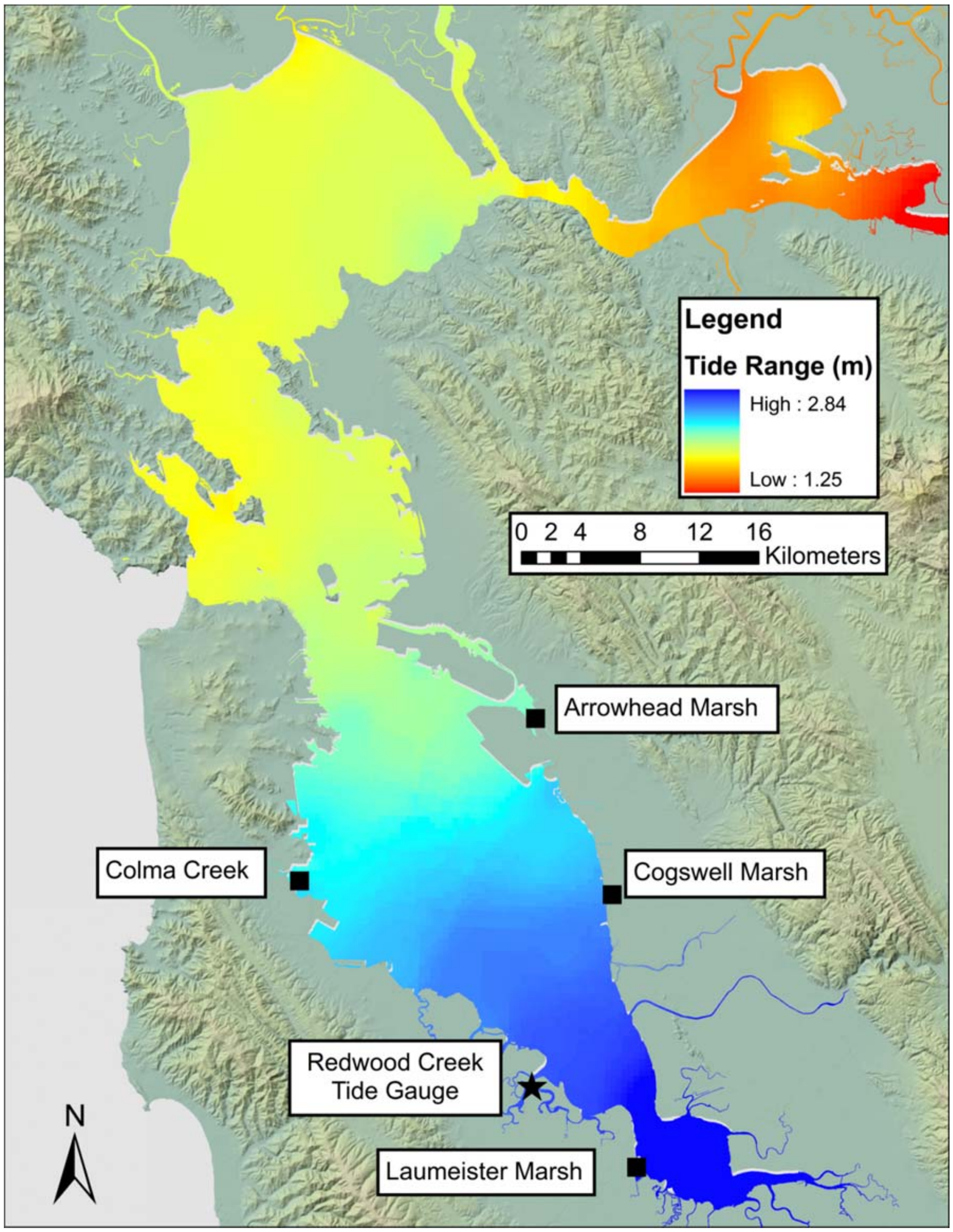


Fig. 1.2 Average monthly change in vegetation elevation (Height above Mean Lower Low Water [MLLW]) at 50 locations in Arrowhead Marsh, Oakland, CA between September 2010 and April 2011. Points represent predicted random slopes for each sample location. The surface elevation of Arrowhead Marsh averages 162 cm in elevation. Mean High Water (MHW) during the winter was 200 cm, Mean Higher High Water (MHHW) was 220 cm, and Maximum Observed Tide Level (MaxHHW) was 240 cm. Plants higher in the tidal prism declined in total height more rapidly than plants lower in the prism; indicating progressive limitation in intertidal refuge cover throughout the winter

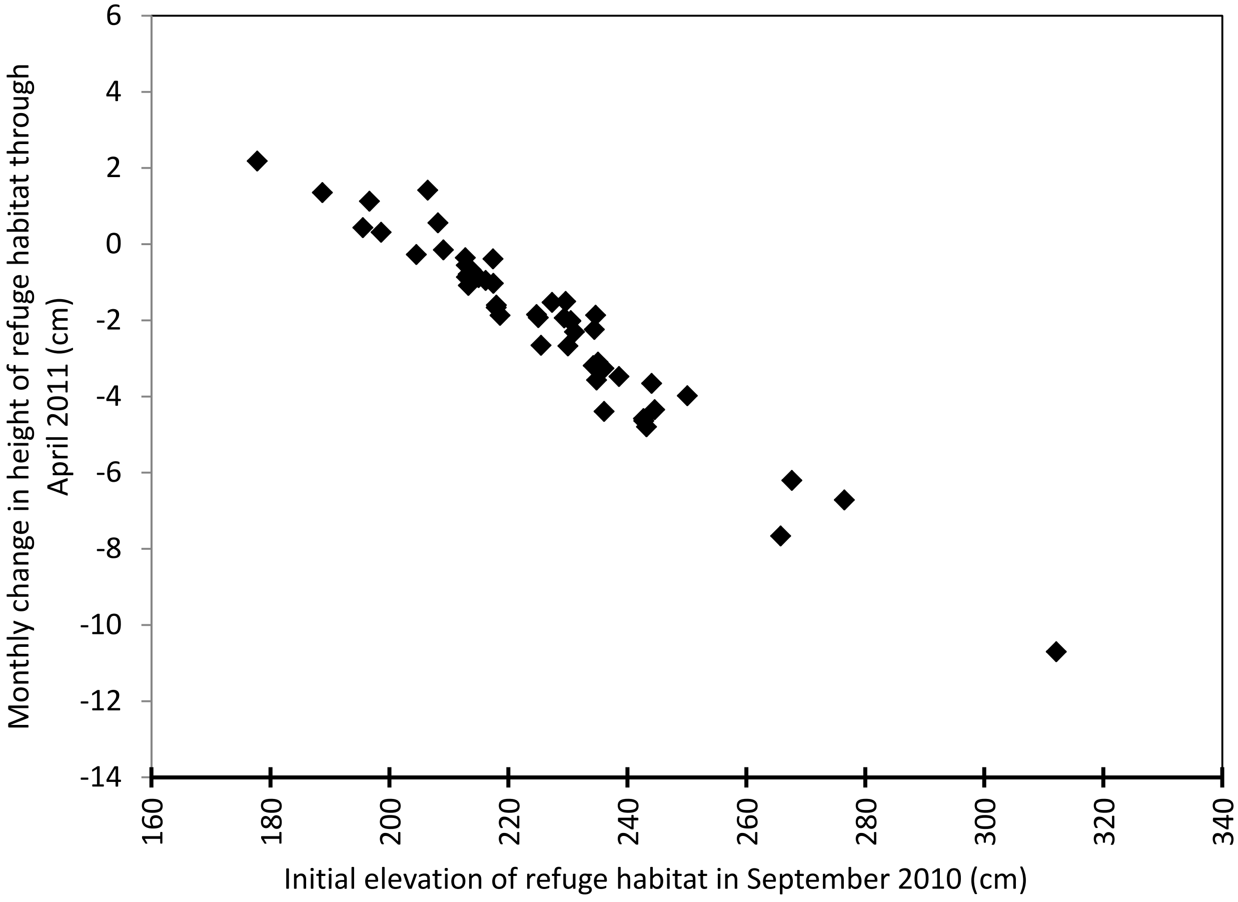


Fig. 1.3 Arrowhead Marsh refuge elevation (marsh elevation plus vegetation height) as proportion of available habitat showing senescence pattern and progressive loss of refuge habitat from September 2010 through April 2011 (n=50). Observed mean high water (MHW), mean higher high water (MHHW), and Maximum observed tide (MaxHHW) indicated by vertical bars

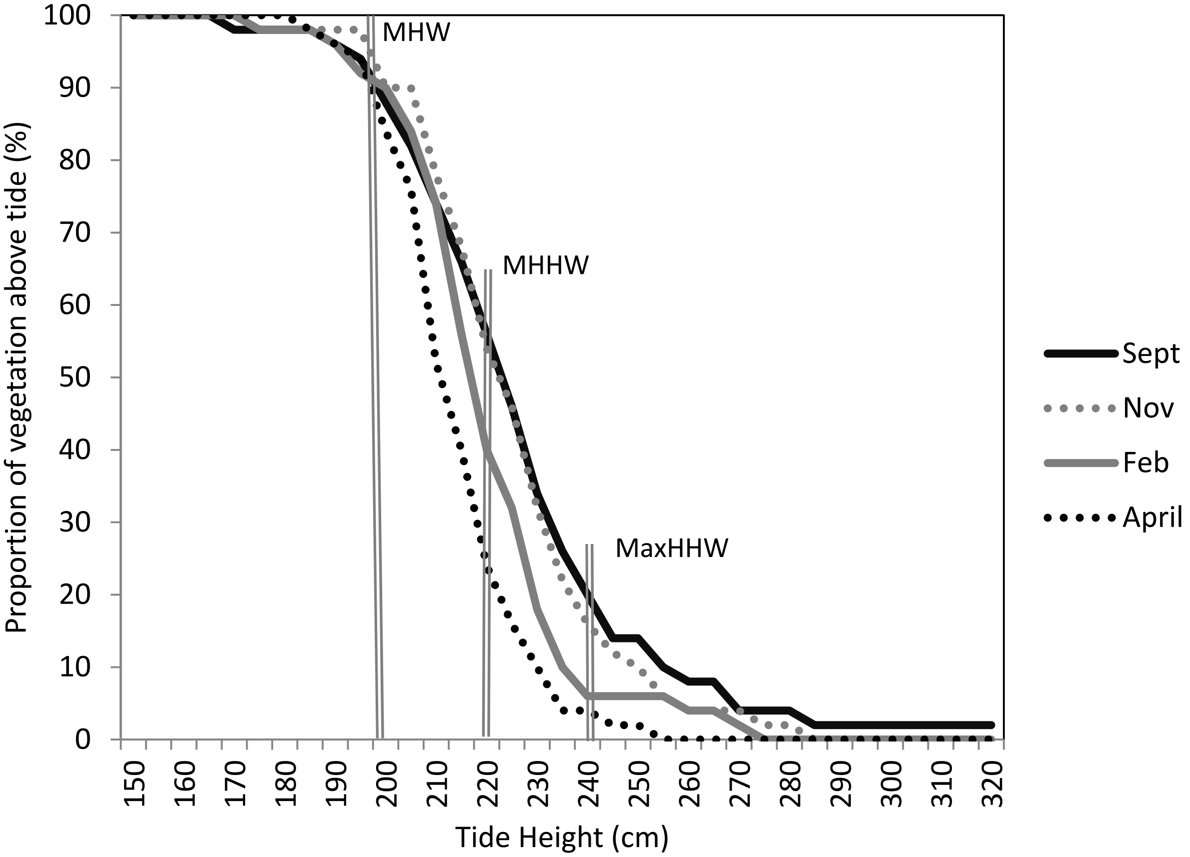


Fig. 1.4 Proportion of habitat above tidal ranges at Arrowhead Marsh (a), Cogswell Marsh (b), Colma Marsh (c), and Laumeister Marsh (d) in South San Francisco Bay in 2004 (Dotted line) prior to *Spartina* eradication and in 2010 after eradication efforts (Solid line)

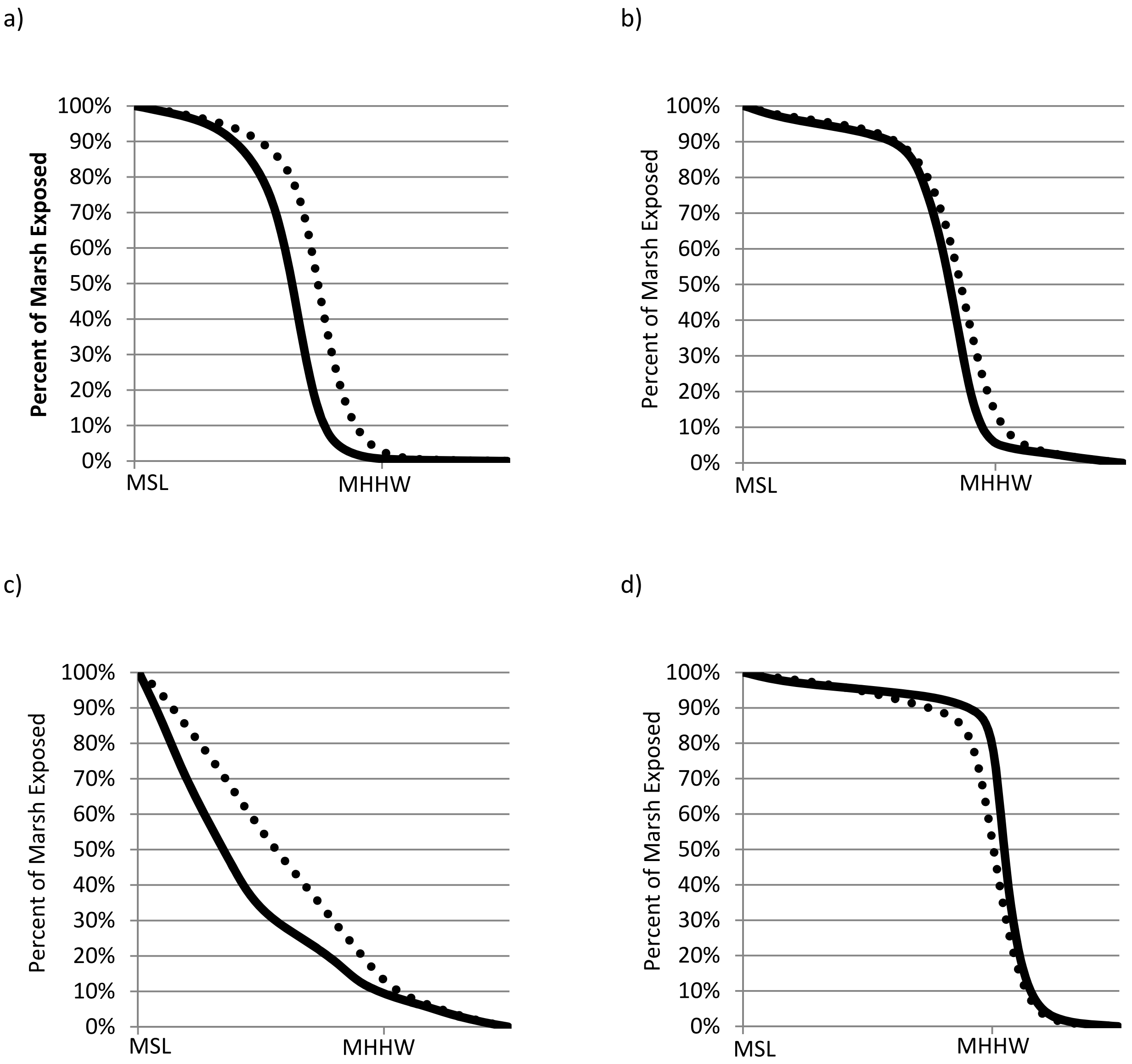


Fig. 1.5 Weekly survival estimates for 3 seasonal periods in relation to Maximum Higher High Water (MaxHHW). Seasonal periods included Winter (November 15 to March 14), Breeding (March 15 to July 14), and Post Breeding (July 15 to November 14). Plotted lines represent observed tide range for each season during this study, 2007-2010

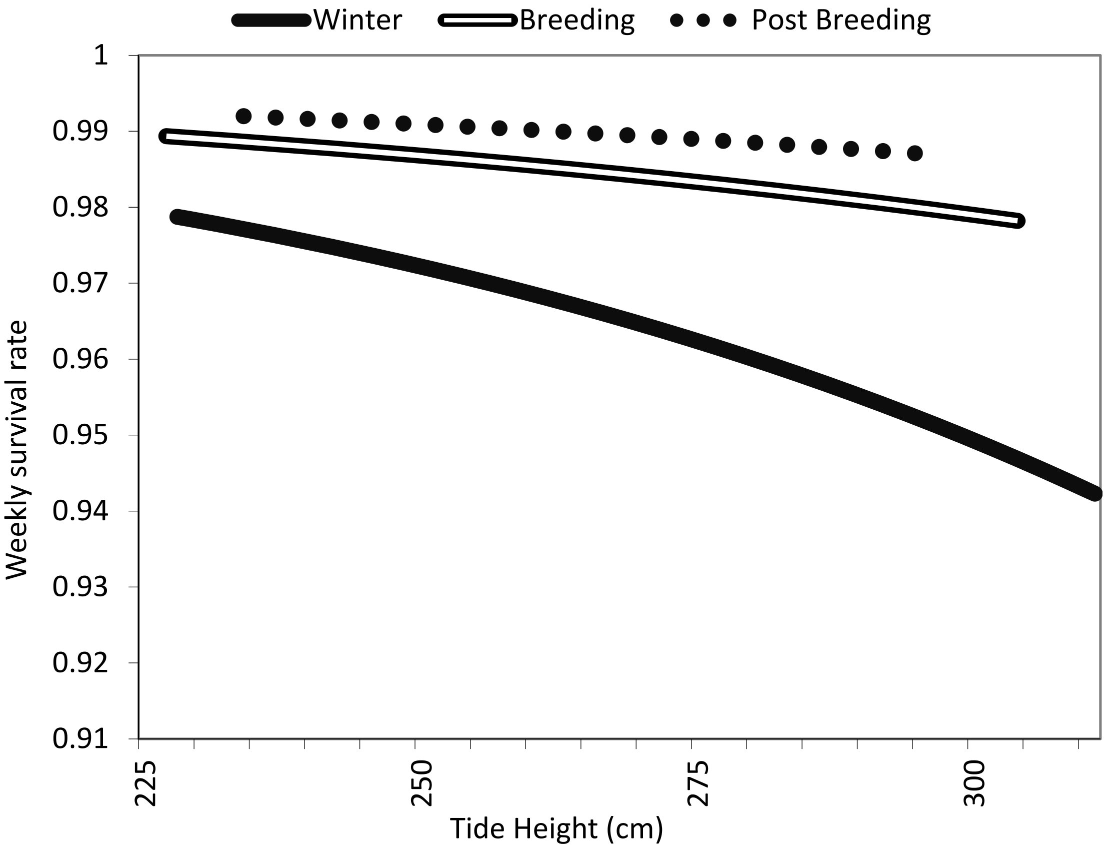
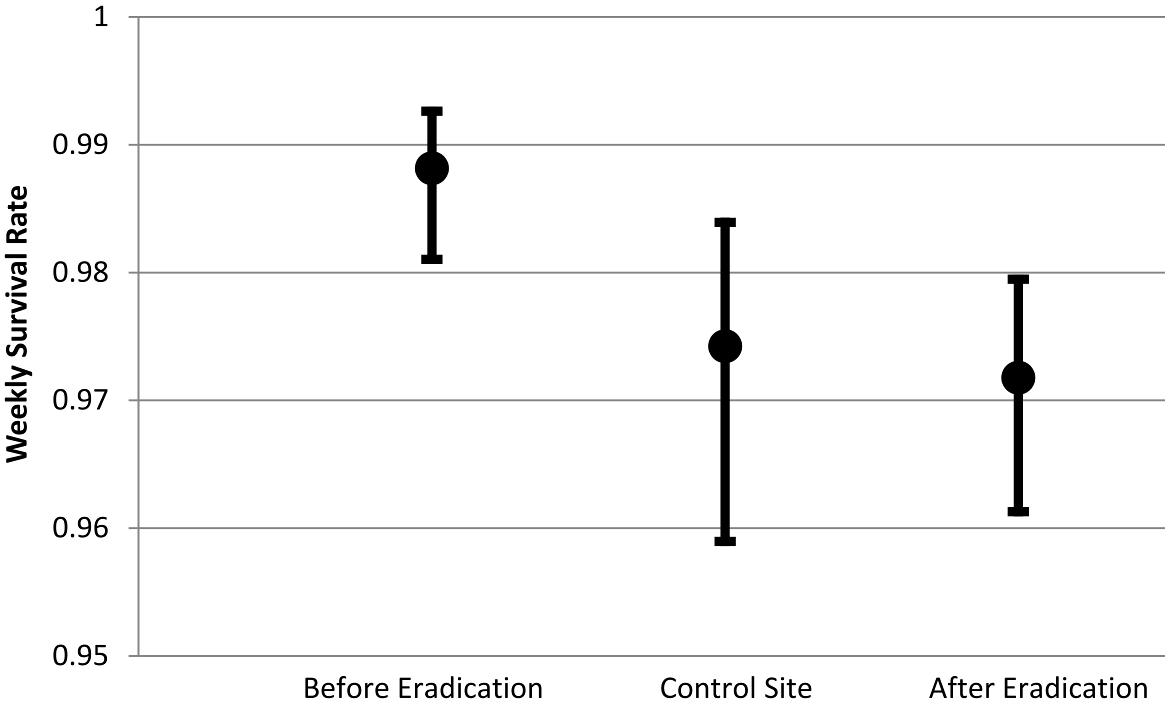


Fig. 1.6 California clapper rail weekly survival rates between January 2007 and March 2010 were analyzed for differences between hybrid *Spartina* treatment groups. The best performing model indicated survival in marshes with hybrid *Spartina* prior to eradication activities (Before) was greater than survival following eradication (After) and at Laumeister which contained virtually no hybrid *Spartina* (Control). Comparison of After to Control groups show equivalent survival rates (95% confidence intervals overlap) and higher survival preceding hybrid *Spartina* eradication (95% confidence intervals do not overlap)



CHAPTER 2: Sea-level rise and the importance of refuge habitats for tidal marsh vertebrates: will artificial islands save the endangered California clapper rail?

Cory T. Overton, John Y. Takekawa, Michael L. Casazza, Thuy-Vy Bui, Marcel Holyoak, Donald R. Strong

ABSTRACT

Terrestrial species living in intertidal habitats experience refuge limitation during periods of tidal inundation, which may be exacerbated by seasonal variation in vegetation structure, tidal cycles, and land-use change. Sea-level rise projections indicate that the severity of this limitation may increase. Artificial habitats that provide escape cover during tidal inundation have been proposed as temporary restoration tools to alleviate these limitations. We tested for evidence of refuge habitat limitation in a population of endangered California clapper rail (*Rallus longirostris obsoletus*) through use of artificial floating island habitats provided during two winters. Previous work demonstrated that clapper rail mortality was especially high during the winter and periods of increased tidal inundation suggesting that tidal refuge habitat is critical to survival. Clapper rails regularly used artificial islands during higher tides and daylight hours. When tide levels inundated the marsh plain, observed use of artificial islands was more than 300 times the expected use based on the area provided. Probability of use varied among islands, and low levels of use were observed at night. These patterns may result from anti-predator behaviors and heterogeneity in either rail density or availability of natural refuges. Endemic saltmarsh species are increasingly at risk from habitat change resulting from sea-level rise and development of adjacent uplands. Escape cover during tidal inundation may need to be supplemented if species are to persist following these changes. Artificial habitats may provide effective short-term mitigation for

habitat change and sea-level rise in tidal marsh environments particularly for conservation-reliant species such as California clapper rails.

INTRODUCTION

Animals living in seasonal or otherwise variable environments often experience temporary limitation in resources leading to reduced survival or reproduction (Elton 1927; Fretwell 1972; Payne and Wilson 1999). These critical periods may create short-term population bottlenecks that influence population dynamics, particularly when seasonal resource limitation increases intra-specific competition or predation (Ekman 1984; Roy and Thomas 2003). Resource supplementation using artificial structures is common practice in conservation, particularly for management of birds and game species (Hinsley and Bellamy 2000; Stoate and Szczur 2001). Artificial structures are credited with increasing populations of waterfowl, osprey, and cavity nesting birds through provision of nest sites (Corrigan et al. 2011; Ewins 1996; Newton 1994). Light-footed Clapper Rail (*R. l. levipes*) management in Southern California involves floating nest structures to augment reproduction (Zembal 1990).

Artificial habitats have also been constructed to improve species' survival rates in a variety of terrestrial and aquatic environments. Hedgerows provide escape cover often increase survival of game birds species and promote greater bird abundance and diversity (Hinsley and Bellamy 2000). Cottontail rabbits (*Sylvilagus* sp.) and snowshoe hare (*Lepus americanus*) used supplemental refuge habitats heavily, but with no apparent change in survival rates (Cox et al. 1997). Artificial rocks increased survival and abundance of velvet geckos (*Oedura lesueurii*; Croak et al. 2013). Artificial sea grass habitats decreased efficiency of predators and increased survival of juvenile walleye pollock (*Theragra chalcogramma*) (Heck Jr. and Thoman 1981; Manatunge et al. 2000; Sogard and Olla 1993). Rearing fish in artificially vegetated hatchery pools may increase survival after stocking (Einfalt et al. 2013). Submerged reef structures may be the most globally widespread artificial habitat enhancement (Seaman 2000). As a management tool, artificial habitats may be a more attractive option than restoration of natural habitat due to the relative flexibility of implementing actions and the immediacy of observable changes in habitat condition. However, artificial habitats may also create ecological traps if predators cue into them and increase their overall capture efficiency (Shochat et al. 2005). Alternatively, avoidance of artificial habitats may result in no net population change and result in costly conservation actions with no tangible results (Smith and Rule 2002).

The ability of natural habitats to provide salt marsh species with refuge cover will decrease as a likely consequence of climate change. Much of the California coast is projected to incur 42-167 cm of sea level rise this century (National Research Council 2012). The natural processes that maintain zones of marsh vegetation, sedimentation and accretion of organic matter, are not likely to keep pace with this rise and 96% of the tidal marsh in San Francisco Bay is projected to convert to mudflat by 2100 (Takekawa 2013). Habitats which do remain will be more frequently inundated and by higher water levels jeopardizing estuarine species (Erwin et al. 2006; Flick et al. 2003). San Francisco Bay currently contains the greatest amount of estuarine saltmarsh along the Pacific Coast (Josseyln 1983; Nichols et al. 1986) despite the loss, fragmentation, or conversion of 80% of this critical habitat (Takekawa et al. 2006). Marshland fill and development of adjacent uplands are likely to have affected the highest elevation marshland resulting in disproportionate loss of tidal refuge habitat. Lack of tidal refuge habitat is particularly problematic for species like the California clapper rail (*Rallus longirostris obsoletus*) and California black rail (*Laterallus jamaicensis coturniculus*) that have small ranges and highly fragmented populations.

The California clapper rail (hereafter, clapper rail) is particularly sensitive to availability of tidal refuge habitats. The state and federally endangered California Clapper Rail is a tidal-marsh obligate species that inhabits primarily lower elevation tidal salt and brackish marshes in San Francisco Bay, California (Albertson and Evens 2000; Gill 1979) and is dependent on refuge cover during high tides for protection from predation. Habitat loss and fragmentation are the major contributors to clapper rail endangerment (Albertson 1995; U.S. Fish and Wildlife Service 2010). Radio-telemetry studies found that clapper rail survival rates were lowest when tide heights were greatest and during the winter when much of the tidal refuge habitat (e.g. *Spartina* sp.) had senesced (Albertson 1995; Chapter 1). An invasive hybrid plant, *Spartina foliosa x alterniflora*, which grows taller and more densely than native vegetation, was associated with increased clapper rail survival rates before the plants were treated with herbicide as part of an eradication effort (Chapter 1). Spread of hybrid *Spartina* within San Francisco Bay reversed the refuge limitation affecting clapper rail populations and resulted in increasing populations prior to the on-going eradication program. The low abundance of clapper rail populations, degraded and fragmented remaining marshland, and additional predicted habitat loss in the future due to continued sea-level rise (Takekawa 2013) imply that on-going management will be necessary to maintain this species (U.S. Fish and Wildlife Service 2010). Since elimination of these threats is not feasible, the California clapper rail is likely to remain a conservation-reliant species maintained through continued management for the foreseeable future (Scott et al. 2005, 2010). One proposed strategy to mitigate low seasonal survival in clapper rails is to provide natural and artificial refuge habitats during the winter. However, evaluating use of these artificial habitats is crucial to understanding their effectiveness as a conservation tool (Smith and Rule 2002).

Our goal was to better understand the importance of tidal refuge habitats for saltmarsh obligate species through habitat supplementation using artificial floating islands. Our approach was to evaluate

California clapper rail use of supplemental tidal refuge habitat in the form of artificial floating islands. Since it was difficult with this endangered species to assess the demographic consequences of artificial island use, we focused our assessment on patterns of use of individual islands. Our specific hypotheses are: (1) use of artificial islands would increase with tide height; and (2) use of artificial islands will increase through time in relation to vegetation senescence, clapper rail habituation, or seasonal relaxation of territoriality.

METHODS

The limited availability of current and future tidal refuge habitat may be alleviated though habitat supplementation, either using artificial material or through intensive restoration. For artificial habitats to be an effective conservation tool they must be used by the species of interest and improve demographic rates. We photo-documented California clapper rail use of artificial floating islands at a marsh suspected of containing limited amounts of tidal refuge habitat.

Arrowhead Marsh is a 10-ha intertidal marsh in San Leandro Bay, Oakland, California, USA. It contains vegetation typical of South San Francisco Bay salt-marshes. Groundcover is a mixture of *Sarcocornia virginica, Distichilis spicata*, *Frankenia grandifolia*, and *Jaumea carnosa*. The primary species providing escape and refuge cover for clapper rails are *Grindelia stricta* and hybrid *Spartina*, with some *Sarcocornia* plants growing tall enough to provide cover (Harvey 1988; Zembal et al. 1989). Arrowhead Marsh also supports one of the highest known densities of California clapper rails. Concurrent population surveys indicated 41-50 clapper rails were present at Arrowhead Marsh in 2010 and 31-36 birds in 2011 (McBroom 2012). Arrowhead Marsh had been the focus of a phased eradication of non-native hybrid *Spartina* from 2007 to 2009 (Hogle 2011). Herbicide treatments to eradicate Spartina in a portion of the marsh began in 2007 but were suspended in 2010 due to uncertainty regarding how vegetation alteration impacted clapper rails. The relatively low elevation of Arrowhead Marsh and habitat change brought about from herbicide application resulted in limitation of tidal refuge habitat particularly during the winter when vegetation senesced (Chapter 1).

Ten 1.5 x 2.1m commercially-available, artificial islands made of recycled plastic and high density foam were deployed in September 2010 along the northeastern edge of Arrowhead Marsh in San Leandro Bay, Oakland, CA, USA (Figures 1-2). Islands were tethered with auger anchors and nylon rope of sufficient length to allow the islands to float during the highest tides but short enough to limit lateral movement. This ensured that the islands provided the same quantity of refuge habitat at all stages of tidal inundation whereas natural habitats provided less refuge habitat as tidal inundation increased. Each island was covered with 1.2-m tall woven-palm screens affixed to a 0.75-m tall PVC frame secured to the island. The extra length of palm screen was overlapped and affixed to the other side, creating a completely enclosed structure with lateral and overhead cover. Openings allowed access for rails on all sides and through the top of the screen but were designed to limit access by avian and mammalian predators.

An infrared camera capable of taking time-elapsed and motion triggered photographs (Reconyx HC600, Holmen, WI, USA) was placed on a small wooden block affixed inside the cover of each island. From October 1, 2010 to March 15, 2011 (Year 1) the cameras took one photograph every minute and could be triggered once every 4 minutes by motion upon which it took a series of photographs at 1 frame per second for 10 seconds resulting in 2.1 million photographs. In a second winter, we lengthened the time-elapse interval to five minutes during November 1, 2011 to March 15, 2012 (Year 2) and took 319,646 photographs. Because of variability between the motion-sensing capability of different cameras, motion-triggered photographs were used only to help interpret photos and not to quantify use. Each photograph was scored for presence or absence, species identification, and number of individuals present in the photograph. We interpolated local tide height at the time each photograph was taken from 6-minute interval tide-height data collected at the NOAA-operated Alameda tide gauge 8km northwest from the study area (National Oceanic and Atmospheric Administration 2011).

We modeled the probability of island use by clapper rails in each year with a logistic mixed effects regression model. Our employment of systematic random sampling to monitor islands (e.g. time-lapse) and high rates of island use by clapper rails were sufficient for logistic regression to provided unbiased estimates of the resource selection probability function (RSPF; Keating and Cherry 2004). That is, our sampling did not bias the probability of use conditioned on habitat covariates and a straightforward interpretation of the RSPF for artificial floating islands was possible (Manly et al. 2002). Fixed effects used in models were tide height, days since island deployment, light cycle (day versus night), and an interaction of tide height with light cycle. Island was included as a random effect factor in models and we established whether a mixed effects model containing random slopes was necessary by comparing Akaike's Information Criterion with a reduced random intercept model (Burnham and Anderson 1998).

We used indicator variables to estimate differences in island use between Year 1 and Year 2 and between daytime use and nighttime use among the continuous variables in the model (tide height and time since deployment). We used contrasts of linear combinations of regression coefficients to determine if the effects of the indicated factor were significantly different from zero on the logarithmic scale (Ramsey and Schafer 1997).

Lastly, we compared the estimated probability of artificial floating island use with the availability of islands as a proportion of total habitat available (i.e. the artificial and natural habitat combined). The RSPF provides a ranking of the importance of each habitat type (Keating and Cherry 2004). At

Arrowhead Marsh, this proportion was 0.016% and RSPF values above this value indicated selection of artificial habitats.

RESULTS

Cameras recorded clapper rails 85,582 times (4.1%) in Year 1 and 6,370 times (2%) in Year 2. Use of islands by a single rail was most common (95.8%), but presumptive pair-bonded rails also simultaneously used islands (4.1%). Photographs captured a single instance of three rails briefly occurring on an island.

The influence of tide height on artificial floating island use by California clapper rails differed between years and between photoperiods but the probability of use was greater than the availability of the artificial habitat at almost any tide level. During Year 2, use of artificial islands was 67% lower (odds-ratio 0.33) during the day and at mean lower low water, represented by the model intercept, than in Year 1 (Table 1). However, tide level increased the odds of artificial island use more in Year 2 than year 1. Every meter of tidal inundation increased the odds of island use 1890% in Year 1 and 2485% in Year 2. The estimated probability of island use at mean higher high water during the day, holding other variables at mean values, was 26.5% in Year 1 and 10.9% in year 2.

Nighttime use of islands was lower in both years (Table 1). Linear contrast of model parameters indicated that tide level did not significantly change the odds of use in either Year 1 (odds ratio 1.22; p = 0.250) or Year 2 (odds ratio: 0.987, p = 0.484). The odds of an island being used increased by 50% every 49 days during Year 1 (Table 1). However, this trend was significantly lower in Year 2 and the odds of use did not significantly change with time (odds ratio 1.0005, p = 0.435). Significant individual variation in use of islands occurred as indicated by the random effect terms (Figure 3a, b).

Selection for artificial floating islands was indicated when the resource selection probability function (RSPF; Figure 3) estimated from the logistic regression model exceeded the availability of artificial islands as a proportion of total habitat (0.016%). The only period for which selection for artificial islands was not evident occurred in Year 2 and during daylight periods when tides levels were below 0.13 m. When tide levels reach the mean elevation of the marsh plain (1.6 m; Chapter 2) the RSPF during the day was 365 times and 106 times the availability of artificial habitats (0.016%) in Year 1 and Year 2, respectively. Equivalent tides at night only provided RSPFs that were 12 times (Year 1) and 2.4 times (Year 2) the availability of artificial habitats.

DISCUSSION

Tidal refuge habitat is a critical component of salt marshes and limitations in its availability may have repercussions, particularly for rare localized species. We suspected that availability of tidal refuge at Arrowhead Marsh was limited due to both recent habitat changes (hybrid *Spartina* eradication) and longer-term changes in relative sea level (Flick et al. 2003). Resident populations of California clapper rail also exhibited survival rate patterns consistent with habitat limitation during high tides and winter (Chapter 1). Our use of artificial floating islands as supplemental tidal refuge habitat provided a unique opportunity to assess the conditions under which an endangered salt marsh obligate species used such habitats.

Two environmental conditions influenced use of artificial islands by clapper rails during both years: tide level and photoperiod. We anticipated that tide level would be a predictor of artificial island use by rails since tidal refuge habitat becomes more limited at higher tide levels. However, we did not anticipate the marked difference in use of artificial islands between daylight and nighttime periods. We also did not expect that tide level would not influence use of islands during the nighttime. We suggest two reasons why selection of tidal refuge habitat by obligate salt marsh species would differ between photoperiods. Firstly, there could be a delay between when habitats are selected and when need for refuge is realized. Winter tides, in San Francisco Bay, are highest during the full and new moons and tide levels peak near the middle of the night when rails are mostly sedentary (Eddleman and Conway 1988). During these periods, lowest tide levels occur near dawn and dusk when rails most actively forage (Nidzieko 2010; Zembal et al. 1989). Selection of habitat at dusk does not reflect the need for refuge habitat once tides rise a few hours later. Clapper rails may have chosen alternative habitat to the islands because there was no need for tidal refuge habitat at dusk or the islands could not be located at night. Secondly, the nocturnal predator community at Arrowhead Marsh may be absent or unable to access marshlands during tidal inundation. Avian raptors frequently occur, and are the primary cause of mortality in clapper rails, at Arrowhead Marsh (USGS, unpublished data). Nocturnal avian predators that could elicit refuge-seeking behavior may not be present at Arrowhead Marsh, although owls are predators of clapper rails elsewhere (Cottam and Nelson 1937; Johnston 1956). Anti-predator behavior in clapper rails may itself be light dependent and the birds may not actively seek refuge in low light conditions if visual predators are absent. This type of plasticity in anti-predator behavior, refuge selection during daylight but not at night, is unknown for clapper rails and may vary according to composition of the predator community as well as with available habitats.

The probability of artificial island use by California clapper rails also differed between years and increased during Year 1. Variation in the amount of naturally occurring tidal refuge habitat may account for these patterns. The tallest vegetation in San Francisco Bay salt marshes is usually native *Spartina foliosa* or hybrid *Spartina* both of which senesce and degrade during the winter (Chapter 1). Progressive limitation in refuge cover could result in increased use of artificial habitats by salt marsh species during the winter. During Year 2, the availability of natural refuge habitat was greater than Year 1 and more vegetation remained above mean high water (USGS, unpublished data). In addition, population density of rails, as indexed by call count surveys, decreased between 2010 and 2011. Fewer individuals within the marsh may also have resulted in lower probability of artificial island use during the second year.

There is increasing concern about the fate of tidal marsh habitats and constituent species in the face of projected sea-level rise (Erwin et al. 2006). Past land use changes that prevent the landward “migration” of salt marsh and reduce the resilience to climate changes have intensified these concerns. In highly developed areas, such as San Francisco Bay, species occupying salt marsh will become reliant on continual conservation actions to enable their persistence. Restoration and rehabilitation of salt marsh habitats may help compensate for the projected effects of climate change but only if the ecological functions needed by species is provided. Escape cover during tidal inundation is one such function that directly influences survival rates of tidal marsh species (Chapter 1). Habitats which provide this function may be disproportionately affected by past land use decisions and future environmental conditions. The utility of artificial habitats as a short-term tool to mitigate these effects may be constrained by the behavior of the target species, presence or abundance of sympatric species, and existing habitat condition.

Species’ behavior and the conditions under which a species selects habitats should be understood to develop an efficient and effective conservation action. For example, artificial islands almost never included more than a pair of birds despite being large enough to hold six or more individuals. A single instance occurred when a third individual, distinguished through external markers used in a separate study, briefly occupied an artificial island before one of the birds already present chased it away. During the highest tides, clapper rails frequently occur in groups when refuge cover is limited in native marshes (Sibley 1955; Stone 1937; Zembal et al. 1989). This lies in contrast to “typical” behavior during other seasons. Territorial contest competition for space governs Clapper rail intraspecific interactions during nesting and brood-rearing periods (Eddleman and Conway 1998). During the short-duration periods when high tides flood the majority of marsh vegetation, scramble competition for refuge habitat is more indicative of behavior. The high density of birds at Arrowhead Marsh may mean that scramble competition for space during high tides limits survival during the winter (Chapter 1). In order for artificial floating islands to alleviate this limitation, the artificial habitats must both be used and provide higher survival probability. Our results clearly indicate that artificial floating islands are used. However, effects on survival rates may be difficult to ascertain due to the unexpected contest competition evident in patterns of artificial island use (i.e. only presumed mated pairs occupying islands). A case-control study would be the most efficient means to detect the effects artificial habitat had on survival rates.

The number and species identity of other species present in salt marsh may also influence the efficacy of artificial habitats. As we previously noted, the presence or absence of specific types of predators (e.g. absence of owls) may have influenced temporal patterns of artificial habitat use by California clapper rails. Specific predators (e.g. corvids) may cue in on artificial habitats which could become ecological traps (Shochat et al. 2005) if survival rates decrease relative to natural habitats. Large artificial habitats could provide protection from tidal inundation for mammalian predators and facilitate their continual occupancy of marshes that otherwise would be inhospitable. Additionally, use of artificial habitats by non-target species may dissuade use by the salt marsh obligates for which they are intended. During the first winter of our study, other species infrequently used the islands and were seen on only 2,325 (0.1%) of photographs. However, during the second winter, non-target species use increased to 7% (21,814) of photographs and was largely due to overnight roosting by American coots (*Fulica americana*). Given the relatively low rate of use by clapper rails during the night in either study year, the use observed by coots may not have influenced clapper rail use. However, this observation illustrates the potential for artificial habitats to be made unavailable to salt marsh species due to occupancy by other species. Other non-target species that used the islands included: Sora (*Porzana carolina*), Canada Goose (*Branta canadensis*), Mallard (*Anas platyrhynchos*), Forster's tern (*Sterna forsteri*), California Gull (*Larus californicus*), Marsh Wren (*Cistothorus palustris*), Salt Marsh Song Sparrow (*Melospiza melodia*), White-crowned Sparrow (*Zonotrichia leucophrys*), Black Phoebe (*Sayornis nigricans*), Snowy Egret (*Egretta thula*), Great Blue Heron (*Ardea herodias*), Norway Rat (*Rattus norvegicus*) and Muskrat (*Ondatra zibethicus*).

The condition of existing habitat, including spatial arrangement of natural tidal refuge, is another factor that may influence the effectiveness of artificial habitats and restoration. Significant variation in use by clapper rails occurred among the islands (Figure 3a, b). While not a specific objective of our project, we note that rails were more frequently observed on islands that were further from the adjacent upland areas. The marshland-upland transition zone is often minimal within the highly urbanized San Francisco estuary and is limited to levees that protect adjacent development. The transition zone at Arrowhead Marsh has been the focus of a rehabilitation project to restore native vegetation. Clapper rails and other salt marsh species are known to use such zones as refuge habitats during extreme tidal inundation (Garcia 1995). Upland transition zones also provide access to marshland for terrestrial predators. Few radio-marked clapper rail mortalities at Arrowhead Marsh could be attributed to mammalian predators (USGS unpublished data). Three factors could explain potential spatial differences in island use: variation in rail density, variation in natural habitat availability, and variation in selection of habitats by rails. Rail density near the upland transition zone is lower and the increased probability of artificial island use further from the upland could be a result of fewer rails occurring near the artificial islands. The availability of natural tidal refuge cover could vary through Arrowhead Marsh if more naturally occurring tidal refuge habitat was available near the upland transition zone, lower use of artificial island could result. However, elevation maps that depict refuge potential in Arrowhead marsh were delineated using LiDAR data collected in February 2010 and do not indicate that more refuge was available near the transition zone (Chapter 1). Similar spatial data is not available concurrent with our study, but we doubt the spatial arrangement of tidal refuge habitat changed substantially. Lastly, natural refuge habitat occurring within the upland transition zone may have been preferred by clapper rails leading to low probability of artificial habitat use. It may be possible to use artificial islands to test the ecological role of different habitat conditions, including presence of alternate refuge habitat types, on the habitat requirements of salt marsh species.

Some San Francisco Bay salt-marshes may currently be limited in refuge habitat. Existing marshes may be able to cope with the projected rise in mean sea level through accretion of sediments and organic matter (Geden et al. 2011; Morris et al. 2002). However, this is not assured and reduction in tidal marsh habitat is expected by the end of the century (Stralberg et al. 2011; Takekawa et al. 2013). Sea-level rise projections also suggest that tidal range will increase (Flick et al. 2003). This would have disproportionate effects on tidal refuge habitat and create additional pressures on populations of salt marsh species. Supplementation of tidal refuge habitats could alleviate short-term demographic bottlenecks and may be critical for long-term population persistence of salt marsh obligate species. Ongoing and future habitat management and restoration in San Francisco Bay should consider provisioning refuge habitats for California clapper rails and other endemic marsh species while accounting for patterns in species behavior and constituent community assemblages.

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TABLES

Table 2.1 Fixed effect estimates of logistic mixed model estimating California clapper rail use of artificial refuge islands October 2010 to March 2011 (Year 1; n=2,095,267) and November 2011 to March 2012 (Year 2; n=319,646) classified for rail presence/absence. Model included random effects of island as a blocking factor (intercept) and random slope regressed against main fixed effects in the model. Year 2 and Nighttime effects were included as factors and parameters are the estimated difference from Year 1 and Daytime factors, respectively.

Effect	Estimate	Std. Error	Z-value	Pr(>|z|)
Intercept	-8.150	0.378	-21.54	<0.001
Year 2	-1.09	0.414	-2.64	0.008
Nighttime	0.938	0.410	2.29	0.022
Year 2.Nighttime	0.420	0.165	2.55	0.011
Tide	2.934	0.298	9.85	<0.001
Year 2.Tide	0.279	0.049	5.71	<0.001
Tide.Nighttime	-2.736	0.026	-105.04	<0.001
Year 2.Tide.Nighttime	-0.490	0.117	-4.17	<0.001
Date	0.00825	0.00284	2.90	0.00367
Year 2.Date	-0.00777	0.000481	-16.14	<0.001

FIGURES

Fig 2.1 Floating artificial islands made of a recycled plastic polymer and high-density foam were installed at Arrowhead Marsh, Oakland, CA in September 2010 and monitored using time elapse and motion triggered cameras through March 2012. Woven palm leaves attached to a PVC frame provided vertical and lateral cover. Each island was anchored just off the marsh plain using auger anchors and braided nylon rope of sufficient length to allow floatation during maximum tide heights (2.5m). Water level in photo is approximately 1.2m for comparison.

Fig 2.2 Ten floating artificial islands (black circles) were deployed on the northeastern shoreline of Arrowhead Marsh in San Leandro Bay, Oakland, California in September 2010.

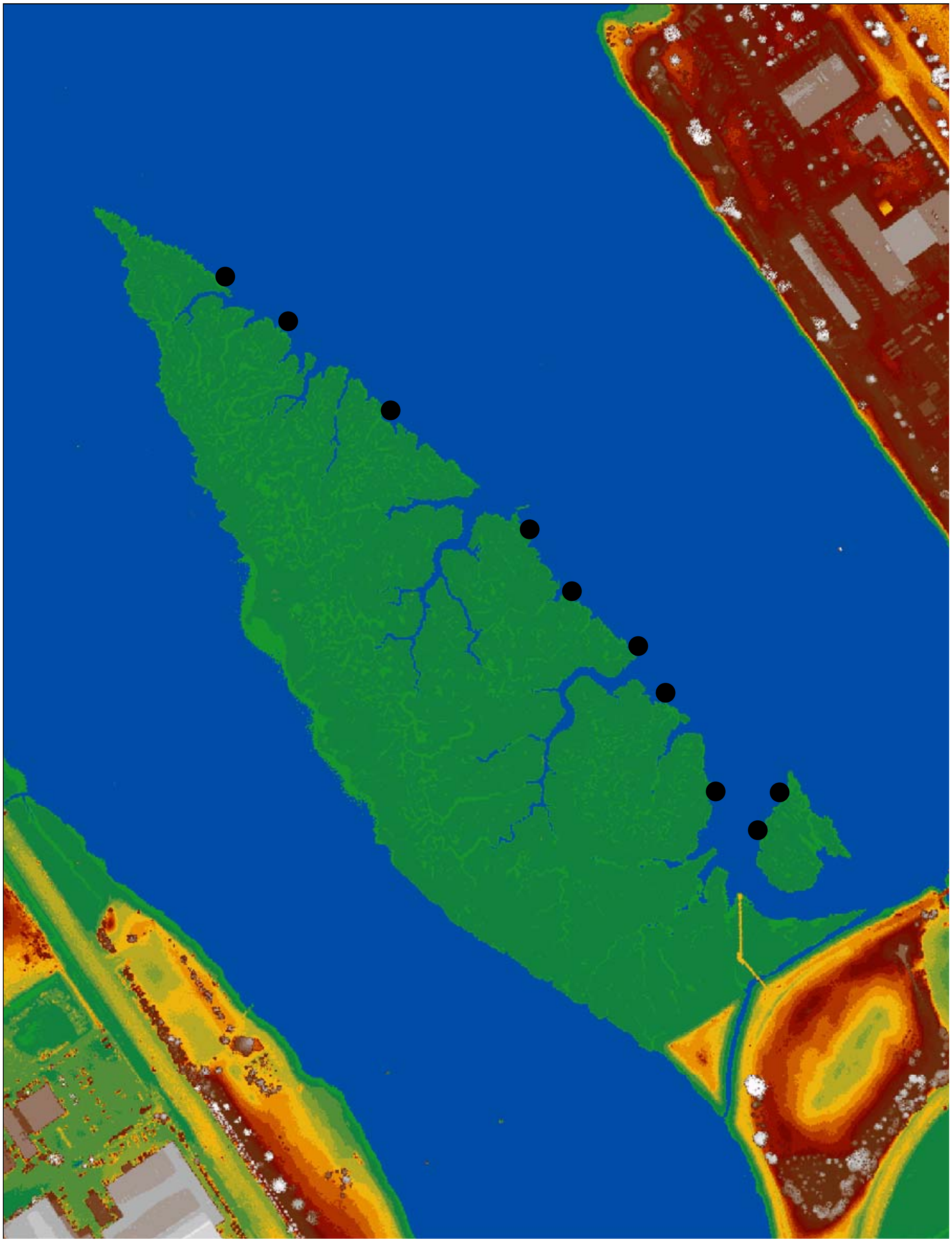
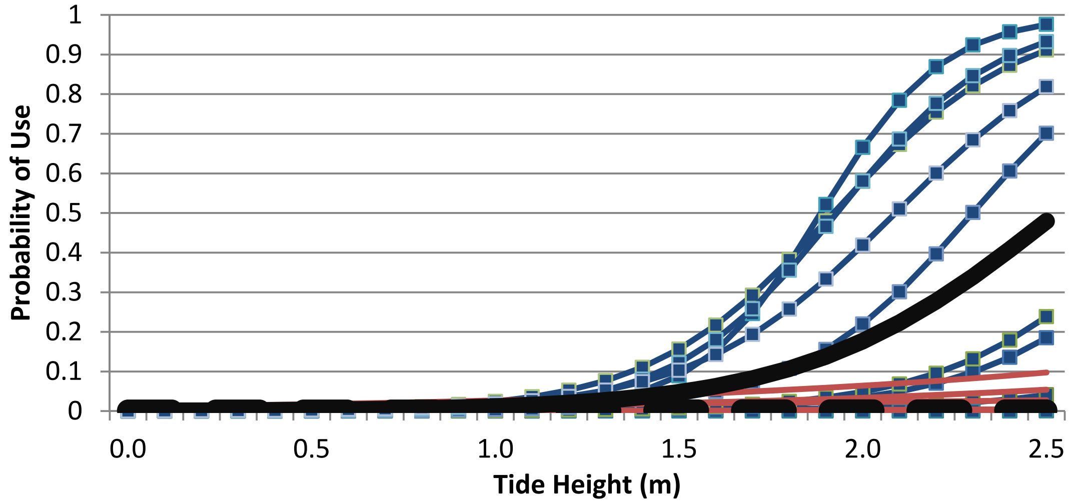
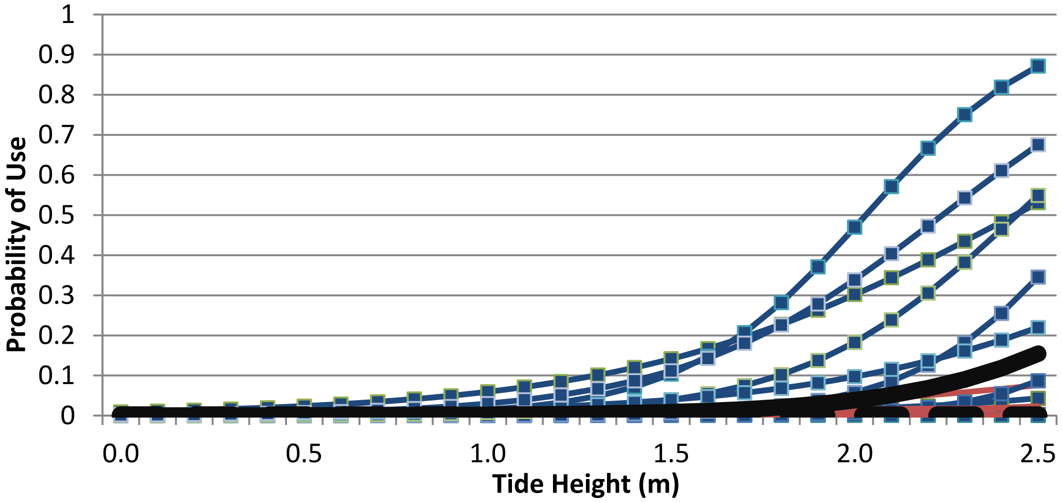


Fig 2.3 Probability of artificial refuge island use between October 2010 and March 2011 (a) and November 2011 and March 2012 (b) by California clapper rails during the day (solid black line) and night (dashed black line) relative to tidal height. Regressions for individual islands included to demonstrate variability in individual island use (daytime = blue lines with squares; nighttime = red lines).

(a)



(b)



CHAPTER 3: Change-point detection prior to kernel analysis improves space use estimation

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ABSTRACT

The process by which most animals use space is rarely static. Animals may change their movement patterns for a variety of ecological and behavioral reasons. When animal locations are subsampled using radio-telemetry to estimate space use the resulting utilization distributions may be biased due to non-stationary, or inhomogeneous, point patterns. This is due to integration of space use estimates across multiple movement phases. We describe a technique incorporating a multivariate, nonparametric change-point detection test before space use is estimated using kernel density analysis using 2,500 simulated radio-telemetry datasets. We term the resulting estimates of space use “change-point utilization distributions”, CPUDs, which provide more accurate estimation of the true underlying movement distribution than traditional kernel density estimates. Since change-points identify shifts in the mean or variance of an individual animal’s locations, CPUDs provide an opportunity to investigate internal and external triggers to change in an individual’s movement process. We examined the timing and potential causes for shifts in the patterns of 100 endangered California clapper rails radio-marked in San Francisco Bay between 2007 and 2010. Change-points in clapper rail movement were associated with a variety of potential triggers including high tides, nesting activity, intrusion by neighboring clapper rails, and transient movements outside the home range.

INTRODUCTION

Understanding where an animal is located is often a prerequisite to infer what resources are being utilized, when such resources are necessary, or why one habitat is used in place of another. Estimates of space use are used to quantify individual and/or population resource use and selection, territoriality, behavior, population density, and response to habitat change (Johnson 1980, Millspaugh and Marzluff 2001, Morales et al. 2004, Moorcroft 2012). Space use estimation from radio-telemetry data has traditionally used some form of Gaussian kernel analysis to estimate a two-dimensional probability surface, or utilization distribution (UD), from animal relocations (Van Winkle 1975, Worton 1989, Laver and Kelly 2008). However, it is increasingly being realized that individuals may not be governed by a single movement pattern for extended periods of time (Mitchell and Power 2004 and 2007, Borger et al. 2006, Moorcroft and Lewis 2006, Fryxell et al. 2008, Wilson et al. 2012). Utilization distributions that cover multiple movement or behavioral states may bias resource selection functions and resulting inference of resource use versus resource availability (Swihart and Slade 1997, Mitchel and Power 2004, Millspaugh et al 2006, Beyer et al. 2010, Wilson et al. 2012). Here, we introduce a new method that incorporates change-point detection prior to kernel analysis and UD estimation. Our approach is suitable for data that are not sufficiently extensive to allow use of advanced methods that require large datasets (e.g. state-space or Brownian bridge models) and when distribution shifts (i.e. multiple movement phases, Nathan et al. 2008) occur in the data (Figure 1).

Recent advancements in technology have allowed collection of animal location data of greater quantity and quality relative to earlier studies. The availability of high frequency, high accuracy data required new developments in the analytical tools to estimate space use patterns, such as Brownian bridge, state-space, and mechanistic models (Horne et al. 2007, Patterson et al. 2008, Kie et al. 2010), which can be used to estimate probability density surfaces to be interpreted as utilization distributions. These techniques rely on high frequency relocation data, often collected via satellites, to estimate movement paths or parameters but this is not always feasible. Animals may be too small for remotely-downloaded satellite tags or recaptured too infrequently for “store-on-board” tags. Satellite tags are also much more expensive than conventional radio-telemetry tags, which are tracked locally. It is rare that a conventional radio-telemetry study can collect sufficient data to use state-space or Brownian bridge modeling. This has left space use estimation from radio-telemetry data with Gaussian kernel analysis as the predominant means used to estimate UDs (Worton 1989, Laver and Kelly 2008).

Space use estimation is a rapidly developing branch of spatial statistics that uses relocations of individuals to quantify probabilities of occurrence. Kernel analysis remains the most popular technique currently used, but other methods exist including delineation of a uniform home range bounded by locations (MCP; Burt 1947, Mohr 1947), nonparametric local convex hull polygons (Getz and Wilmers 2004), characteristic hull polygons (Downs and Horner 2008), and Brownian bridge models (Horne et al. 2007). In most applications, the resultant utilization distribution is intended as an estimate of a single sub-sampled movement process (Moorcroft and Lewis 2006, Fieberg 2007a, Kie et al. 2010) or movement path (Horne et al. 2007). However, none of the above approaches identifies stationary point patterns and result in biased space use estimates (Downs et al 2012). By contrast, state-space models use high frequency relocation data to describe the attributes of the movement process itself (using biased/correlated random walk sub-models) which may include multiple independent states (movement phases) and the probability of transition between these states (Patterson et al. 2008).

The ability of state-space models to account for these changes in the movement process (e.g. changes in animal behavior; Morales et al. 2004) provides a means to develop realistic predictive models of animal space use (Johnson et al. 2008). However, we know of no analogous method to identify state changes or homogenous point patterns for kernel analysis or for any other method of utilization distribution estimation. Keating and Cherry (2009) developed a method to modify the smoothing parameter used in a kernel analysis by using a temporal covariate. This is an improvement to kernel analysis when space use varies in time, but does not provide estimates of space use during individual movement phases/behavior states and may not accurately represent space use if change is not incremental. Point process clustering identifies unique spatial clusters in animal locations (Mane et al. 2005) but these and similar techniques ignore the sequential nature of movement when estimating distributions.

The main method by which temporal variation in distribution is handled in a typical kernel analysis is subjectively dividing locations of an animal into seasonal or behavioral groupings prior to UD estimation. One purpose of this grouping is to isolate stationary movement processes. Failure to do so can have large impacts on UD estimates and resulting inferences about resource selection (Borger et al. 2008, Beyer et al. 2010, Swihart and Slade 1997). However, subjective classification into different seasons may risk not identifying all movement phases in the data. Classification of a breeding season in a breeding bird, for example, may actually include a movement phase corresponding to an incubation stage, activity during nesting, and brood care following hatching. In other words, the "cognitive map" used to identify resources within an individual's home range may change rapidly (Powell 2000). Furthermore, switches in movement phase may not occur simultaneously for all individuals studied. Although subjective assignment of phenological movement patterns may be obvious, such as for migrating species, not all changes in movement phase are likely to be as apparent.

Change point detection is used in many fields to identify distributional shifts in time series and many methods are available for analysis (Lung-Yut-Fong et al. 2012, Reeves et al. 2007). We propose initially using a nonparametric, multivariate change-point detection method to identify homogenous point patterns (Downs et al 2012) followed by weighted kernel analysis for space use estimation (Fieberg 2007b); hereafter, called change point utilization distributions (CPUDs). Most alternative techniques to estimate change points either are unsuitable for multivariate (x,y) coordinate data (Hawkins and Deng 2010, Pettitt 1979) or assume the data is normally (or otherwise identifiably) distributed (Lavielle and Teyssiere 2006, Maboudou-Tchao and Hawkins 2013), which is unlikely in radio-telemetry datasets. Bayesian change point detection (Cheon and Kim 2010) and the nonparametric Wilcoxon rank statistic (Lung-Yut-Fong et al. 2012) may provide analogs to the technique presented here and could be investigated. The change-point detection method we develop here uses the Craemer test statistic (Baringhaus and Franz 2004, Franz 2006) to test non-parametrically for changes in the mean or variance of location coordinates sequentially through the data. This serves to identify changes in the movement process (Figure 1) rather than non-sequential patterns identified by traditional clustering methods or gradually adapting the smoothing parameter (Keating and Cherry 2009). We simulated radio-telemetry relocation datasets that incorporated a range of distributions and movement phases and contrast CPUDs with conventional UDs generated using kernel density estimation without change point clustering. In addition to providing utilization distributions that did not integrate space use estimates across different movement phases, our method also provides a second important output, the identified change points which can be subsequently investigated for timing and cause of movement phase changes. To illustrate the additional questions that change point timing can answer, we used a dataset of radio-marked California clapper rails (*Rallus longirostris obsoletus*) tracked in San Francisco Bay between 2007 and 2010 to identify potential causes and test for temporal patterns of change point occurrence.

METHODS

We used simulated data to compare the accuracy of utilization distributions developed using traditional kernel estimation with those developed from change-point kernel analysis. We generated simulated data from known probability distributions, and so we could obtain exact measures of UD performance. Probability distributions representing a movement phase were randomly centered in a 400x400-unit grid with locations drawn from a bivariate exponential power distribution with scale and shape parameters drawn from gamma distributions (Gam(10, 12); Gam(0.5, 4), respectively) using Program R (Solaro 2004). Median values from these distributions corresponded to a 120-unit average dispersal distances from the center of a movement phase and high degree of overlap when multiple movement phases occurred in the data (Figure 1). We simulated radio-telemetry location data for 2,500 individuals where each individual was randomly assigned 30-375 relocations distributed in 1 to 5 movement phases. The only additional constraint was that each movement phase had to contain at least five locations; the minimum needed to calculate subsequent utilization distributions. The bivariate exponential power distribution is flexible and can represent distributions that are sharply peaked at the center to nearly a circular uniform distribution (Horne and Garton 2006). Our selection of Gamma distributions from which to draw the shape and scale parameters used in the bivariate exponential power distribution resulted in median shapes that were approximately circular normal but allowed for some variation in individual movement phases.

We tested for differences in the mean and variance of the X- and Y-coordinates using the multivariate, nonparametric Craemer test at each interval in the sequence of relocations for each individual (Baringhaus and Franz 2004, Franz 2006). The maximum Craemer test statistic identified a single change point in the sequence of locations and was run iteratively until no further change points were discovered at a specific alpha level. A subsample of 500 individuals was analyzed using four alpha levels (0.1, 0.05, 0.01, and 0.001) to determine error rates, as described below. Performance of the Craemer test at each alpha level was assessed using the number and type of errors in estimating change-point locations. Four types of errors were identified:

1. Errors of omission occurred when a change point should have been detected but was not; resulting in “clumping” two separate movement phases.
2. Errors of commission occurred when a change point was detected where no change in the movement phase occurred, resulting in “splitting” a single movement phase.
3. Errors of both commission and omission occurred when a change point is detected at the wrong point in the relocation sequence; resulting in the splitting of one movement phase into two, half of which is clumped with an adjacent process.
4. Errors in the location of a switch are identical to the errors of commission and omission where the specific timing of a change point is slightly different from the true timing of the change point.

“Switching errors” are likely to have minor effects on the resulting UD estimates unless sample sizes are low. When a change point was estimated within five locations of where the true movement phase change occurred we categorized the error as a switching error. Errors of commission and omission were identified when the estimated change point was greater than five locations from the true movement phase change. The standard of five locations that we used to distinguish between switching errors and errors of commission and omission is subjective, but allowed us to investigate whether minor errors in the position of change point detection had different impacts on utilization distribution estimates than either greater errors or correct change point detection. Once an appropriate alpha level was determined, change point detection was completed for all individuals.

Two utilization distributions were calculated for each individual; one using traditional Gaussian kernel analysis on the entire set of locations for each individual (hereafter, “Full UD”) and a second using weighted kernels (Fieberg 2007b) developed for each movement phase identified during change point detection (hereafter, “CPUD”). The weights used to calculate the CPUD were equal to the proportion of total locations for an individual occurring in the movement phase. We used the least squares cross validation derived smoothing parameter (Worton 1989) for all kernel analysis.

The random locations for each movement phase were drawn from a known distribution; therefore, we could calculate the true probability density function (PDF) for the set of relocations. We used the volume of intersection index (VOI; Fieberg and Kochanny 2005) to calculate the proportion of the true PDF that was estimated by the Full UD and CPUDs. The VOI index ranges from zero when two distributions do not overlap to 1 if the distributions are identical. The difference between the Full UD and CPUD VOI values measures the difference in the accuracy of each utilization distribution and values near zero indicate both methods equally estimate the movement process.

We tested how differences in accuracy between Full UDs and CPUDs were affected by properties of the underlying movement process. Specifically, we investigated whether incorporating change-point detection outperformed traditional kernel analysis with respect to: the true and estimated number of movement phases, mean distance between movement phase centers, parameters describing the shape of the actual movement phase, and sample size. We further quantified the amount of overlap in estimates of core areas (50% volumetric isopleth) between Full UDs and CPUDs since this region typically has the greatest influence (i.e. probability of use per unit area) on subsequent resource selection functions (Millspaugh et al. 2006).

In addition to estimates of space-use that are unbiased by changes within the movement process of an animal, CPUDs provide an opportunity to investigate causes and consequences of movement phase shifts. Prior studies of California clapper rail space use have used three seasonal periods to identify temporal variation in home range size (Rohmer 2010). We investigated whether change points in clapper rail movement patterns correspond with the start of these seasonal periods (March 15, July 15, and November 15). We tracked 100 radio-marked California clapper rails fitted with 9.5-gram VHF transmitters in four San Francisco Bay salt marshes between January 2007 and September 2010. Individuals were remarked every year and tracked until mortality or early failure of radios. Locations were estimated approximately every other day by triangulating 3-5 bearings taken using handheld three element Yagi antennas at a distance of 10-200 meters. We identified change points within each individual's set of relocations then tested whether change point occurrence was greater during the months previously used to delineate seasonal patterns in clapper rail space use (March, July, and November).

Change points may also be used to identify the reasons underlying an individual's changed space use patterns. This can reveal important information about the quality of habitats and potential effects on the population dynamics of territorial species (Adams 2001). For example, territory size may be inflexible or size may vary with fluctuations in available resources, such as food availability, leading to either stable or fluctuating population densities when space for territories is limiting (Adams 2001). Territories may also fluctuate due to interactions between neighbors and other external factors or internal states of the focal animal (Nathan et al. 2008). We assessed 4 categories of potential causes for clapper rail change points: dispersal and transient movements; internal triggers; intraspecific triggers, and external triggers. Change points associated with dispersal events were obvious because clapper rail habitat in San Francisco Bay is fragmented and movements to disjunct marshland are rare and require uncharacteristic long distance movements. Clapper rails are highly secretive and not easily viewed, therefore, we only assessed one internal trigger, nesting activity, which could be identified from ancillary data (nests discovered for radio-marked birds) and inferred from movement patterns (small territories occurring during the breeding season). Intraspecific triggers included interactions with known mates (i.e. both individuals of a mated pair were radio-marked) and interactions with neighboring rails (i.e. neighboring individuals were both radio-marked). External triggers included the death of a mate to predation and occurrence of high tides. Inundation of tidal marsh affects California clapper rail survival and habitat selection and is likely to affect movement patterns as well (Chapters 1 and 2). We identified the highest 10% tides observed in San Francisco Bay concurrent with telemetry (National Oceanic and Atmospheric Administration 2013) and whether change point occurred on days with these extreme tide events. Furthermore, we used a Chi-square test to determine if the probability of change points occurring on a day with the 10% highest tides was greater than expected if change points occurred irrespective of tide level.

RESULTS

Analysis of the sensitivity of the Craemer test to different alpha levels revealed that the highest accuracy in change point detection occurred using an alpha level of 0.01 (Figure 2). Higher alpha levels (0.05 and 0.1) resulted in increased rates of errors of commission and the lower alpha level (0.001) resulted in increased rates of errors of omission. The rate of switching errors was relatively constant across all alpha levels evaluated. Therefore, we assessed the Craemer test statistic using an alpha level of 0.01 in all subsequent analyses.

Change-point detection often resulted in inaccuracies in the number or location of change-points. The simulated datasets contained 4,871 change-points (i.e. the number of movement phases minus 1) and the Craemer test detected 5,129 change-points (Table 1). The Craemer test identified the correct number of movement phases for 59.4% of simulated datasets and data with fewer true movement phases were more likely to be accurately estimated than data with more movement phases (Table 1). Since the probability of error in change-point detection is compounded the more change points occur, a lower proportion (47.6%) of datasets had all change-points estimated correctly (42.1%) or with only minor switching errors (5.5%). Datasets that had only incorrect change-points detection were less frequent; errors of commission occurred in 7.9% of individuals, errors of omission occurred in 6.2%, and a combination of both errors occurred in 9.6%.

Both Full UDs and CPUDs estimated most (81.3% and 84.5%, respectively) of the true movements phase distribution from which locations were sampled (Figure 3). The difference in paired VOI indices, which measure the relative accuracy of the two kernel analysis techniques, indicated the CPUD estimated 3.3% more of the true movement process on average. When no change-points were detected (19.3% of individuals; Table 1) both techniques provided identical UDs. CPUDs estimated space use more accurately than traditional kernel analysis for the majority (63.6%) of individuals and average improvement for these individuals was 5.4%. Full UDs outperformed CPUDs for only 15.5% of individuals and the average improvement in the true movement process estimate was 1.1%.

Relative performance of the CPUD and Full UD methods suggest substantial improvement in space use estimation using CPUD. CPUDs performed better than Full UDs at estimating the true movement process when the correct number of change points were estimated, but even when the incorrect numbers of change points were estimated improved space use estimates occurred (Figure 4). When no change points were detected, the Full UD and CPUD were identical and there was no difference in the VOI indices. Estimation of the movement process using CPUDs was more accurate regardless of the number of true (Figure 5a) or estimated (Figure 5b) movement phases present in the data. Neither the number nor type of errors in estimating change points using the Craemer test had a strong relationship to the increased accuracy of the CPUD (Figures 6). CPUDs and Full UDs often identified different areas as territory “cores” (defined by an isopleth encompassing 50% of kernel density) the extent of these differences increased as more movement phases were present in the data (Figure 7). Dissimilarity between the Full UD and CPUD was associated with increased relative performance of the CPUD technique (Figure 8).

Relative performance of the CPUD method was largely unrelated to attributes of the underlying movement processes used to simulate the data. Even though we constrained the center of movement phases to a small area, change-point detection was easier when movement phase centers were further apart and CPUDs resulted in slightly more accurate estimates of space use (Figure 9). There was no relationship between CPUD performance and either the shape or the scale parameters of the true movement phase(s) used to generate the simulated locations or with the total number of locations in the simulated data. However when one or more change points were detected for an individual, CPUD resulted in significant improvement in space use estimation even when the minimum samples size of any single movement phase was small (Figure 10).

California clapper rail telemetry data (100 individuals; 15,392 locations) had 341 change points identified using the Craemer test, resulting in 441 CPUDs. The number of change points per individual ranged between 0 and 14. The average daily probability of a change point occurring was 2% (95% CI: 1.7 to 2.2) and did not differ between months ($\chi^2 = 2958.9$, d.f. = 15380, $p \approx 1.0$; Figure 11). Potential triggers to movement were identified for 157 (46%) change points and including multiple potential causes for some change-points (Table 2). The most common identified cause involved transient movement, Burt's (1943) "occasional sallies" which were identified with 55 (16%) of change points. Dispersal of California clapper rails was uncommon and only 3 (1%) change points were associated with dispersal events where a rail established a territory in a different marsh than it was marked in. Confirmed or assumed nesting activity was categorized for 56 (16%) of change points. Intraspecific interactions triggered change points when individuals formed or dissolved pairbonds prior to nesting, colonized areas formerly occupied by neighbors or were displaced by other individuals and occurred 19 (6%) times. Death of a known mate was responsible for 2 change points, and 40 (12%) change points occurred on days with the highest 10% of observed tides during the study. Change points did not occur randomly with respect to tide height ($\chi^2 = 22.65$, d.f. = 1, $p < 0.001$). The probability of a change point occurring during the highest 10% of tides was 4.5% (95%CI: 3.1 to 5.9). When tides were lower, the probability of a change point occurring was 2% (95%CI: 1.8 to 2.3).

DISCUSSION

Advances in radio-tracking technology have resulted in smaller devices capable of obtaining location data of greater quantity and quality on a wide variety of species (Cagnacci et al. 2010). Statistical methods to analyze these extensive dataset have improved as well, allowing movement path estimation (Brownian Bridge; Horne et al. 2007) and mechanistic models incorporating state changes in movement characteristics (state-space models; Patterson et al. 2008). However, the technological advancements are still not available or suitable for a wide variety of species, and kernel analysis remains a common means to investigate home range, territoriality, behavior, and resource selection of individuals. A chief advantage of state-space models is the identification and estimation of separate movement patterns present within the data. Recognition that space use patterns may change throughout the year led to development of kernel methods that incorporate temporal change in estimates of utilization distributions using a circular, time-based, covariate to the smoothing parameter (Keating and Cherry 2009). This method has been used to model intra- and inter-annual distribution of bird recoveries in Europe (Calenge et al. 2011) and works well when distributions change incrementally. However, abrupt changes in patterns of space use, as well as the events that trigger such changes, may be of interest.

The merging of change-point detection with kernel analysis provides a new mechanism to study when and why individuals modify their use of habitats. Rather than a single estimate of space use, CPUDs provide timing of change points and UDs that may correspond to particular internal states of interest (i.e. resource needs or behaviors; Nathan et al. 2008). Occurrence of change points can be analyzed across a population of marked animals to identify behavioral (e.g. nest initiation) or environmental (e.g. tide level) triggers to different movement phases (Giuggioli and Bartumeus 2010). A similar approach is available for state-space models when investigating covariates to transition probabilities (McClintock et al. 2012). Since CPUDs identify individual movement phases, comparisons of space use under particular behavioral (e.g. incubating vs. brood rearing) or environmental constraints are possible. This is of particular concern when UDs are subsequently used in resource selections functions (Millspaugh et al. 2006) and/or use-availability designs (Beyer et al. 2010). Resource selection functions of radio-marked coyotes (*Canis latrans*) with behavior incorporated into UD development resulted in markedly different interpretation of habitat use and needs compared to “naive” UDs (Wilson et al. 2012). Lastly, CPUDs may allow for additional comparison between individuals relating the movement strategy employed; for example, survival rate difference of nomadic individuals versus sedentary ones.

Our simulated data suggests that change point detection has little downside risk to space use or utilization distribution estimation even when error rates are moderately high. Using change point detection prior to kernel analysis resulted in greater accuracy of estimated UDs and was primarily due to change in location of core areas. We also identified modest improvement in CPUDs with increasing distance between movement phase centers. Within our simulated data, the average dispersal distance from the center of simulated movement phases was 120 units while all movement phase centers were constrained to occur randomly within a 400x400-unit grid, indicating most movement phases would have overlapped considerably. The lack of spatial segregation in our simulated data also explains why change point detection was relatively poor. Discontinuous movement phases would result in even greater performance using the CPUD method.

Many studies have provided recommendations on minimum sample sizes necessary for unbiased kernel analysis (Seaman et al. 1999, Borger et al. 2006, Laver and Kelly 2008, Fieberg and Borger 2012). CPUDs outperformed traditional kernel analysis even with as few as five locations being used to estimate individual movement phases. We recognize that considerable variability in space use patterns may exist within and between species and the best strategy may be to collect locations with sufficient frequency that even the shortest expected movement phase is adequately represented. Alternatively, transient movement phases represent a behavior state quite different from Burt’s (1943) original, and often referenced, definition of a home range: “…that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range” (Burt 1943 Powel and Mitchell 2012). The operative word “normal” has been much debated in home range literature (Kie et al. 2010, Osborn 2004, White and Garrott 1990). Transient movement phases represent the “occasional sallies” referenced by Burt (1943). These transient movement phases are not identifiable by traditional kernel analysis; however, change point analysis can identify these short duration movement phases for exclusion when estimating home ranges.

The once ubiquitous application of conventional radio-telemetry to address critical questions regarding species’ space and resource use has been eclipsed by new technologies and subsequent methodologies for analyzing high frequency, high accuracy locational data. These new methods can incorporate increased flexibility and realism by recognizing that individuals do not move nor use space equally at all times and subsequently investigate why this is so (Fryxell et al. 2008, Patterson et al. 2008). Our technique is suitable for investigations of space use and resource selection using radio-telemetry data on a wide variety of taxa and mirrors rapidly developing analytical techniques currently only available for use with very high frequency locational data. Our incorporation of a change point estimation technique with kernel analysis identified differences in the distribution, either location and/or spread, of animal locations. The resulting UD estimates are equal to traditional kernel analysis when no change points occurred and UD estimates are more accurate when multiple movement phases occur in the data.

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TABLES

Table 3.1 Number of true movement phases and estimated movement phases (i.e. number of change points + 1) for simulated radio-telemetry data. Most data sets identified the correct number of movement phases (underlined) though the proportion identified correctly decreased as the full movement process became more complex (i.e. more movement phases occurred in the data).

	Estimated clusters	1	2	3	4	5	6	7	8	9	Total
True number of clusters											
1		**82.0%**	13.9%	3.6%	0.4%	0.2%	0.0%	0.0%	0.0%	0.0%	534
2		5.7%	**70.1%**	17.2%	5.3%	1.4%	0.4%	0.0%	0.0%	0.0%	495
3		1.0%	13.6%	**56.5%**	21.0%	6.2%	1.4%	0.2%	0.0%	0.0%	499
4		1.6%	3.5%	22.9%	**47.5%**	20.8%	2.7%	0.8%	0.2%	0.0%	510
5		0.9%	4.1%	6.9%	23.6%	**38.3%**	18.8%	5.6%	1.5%	0.2%	462
Grand Total		**19.3%**	**21.0%**	**21.4%**	**19.4%**	**12.9%**	**4.4%**	**1.2%**	**0.3%**	**0.0%**	**2500**

Table 3.2 Potential causes of change points identified for California clapper rails radio-marked from January 2007 to September 2010 in San Francisco Bay, California.

Change Point Cause	Number of Occurrences	Proportion
Dispersal	3	1%
End of Transient Movement	41	12%
Internal - Nesting	5	1%
Internal - Nesting complete	4	1%
Internal - Assumed nesting	29	9%
Internal - Assumed nesting complete	10	3%
External - Mate Death	2	1%
External - New Pairbond	2	1%
External - Pairbond, following mate	1	0%
External - Colonization of vacant territory (movement or death of neighbor)	2	1%
External - Intraspecific Displacement	10	3%
External - Tide	30	9%
Multiple; End of Transient Movement and Internal - Nesting	1	0%
Multiple; End of Transient Movement and Internal - Assumed nesting	3	1%
Multiple; End of Transient Movement and External - New Pairbond	3	1%
Multiple; End of Transient Movement and External - Tide	7	2%
Multiple External -Tides and Internal - Assumed nesting	3	1%
Multiple Internal - Assumed nesting; External - Intraspecific Displacement	1	0%
Unknown	184	54%
Total	**341**	

*Nesting assumed if change point occurs April 1 and August 31 and territory (95% contour of UD) is less than 2ha in size. Any bias would be toward overestimating the frequency of nesting.

FIGURES

Fig 3.1 Traditional kernel density estimation (KDE) incorporates all relocations for an animal to develop a utilization distribution (a). When multiple movement phases occur within the set of relocations, change point analysis prior to KDE identified shifts in the distribution of locations allowing estimation of state-specific utilization distributions (b)

a)

b)

Fig 3.2 Change point assignment of 1000 simulated radio-telemetry datasets using multiple alpha levels to evaluate the Craemer test

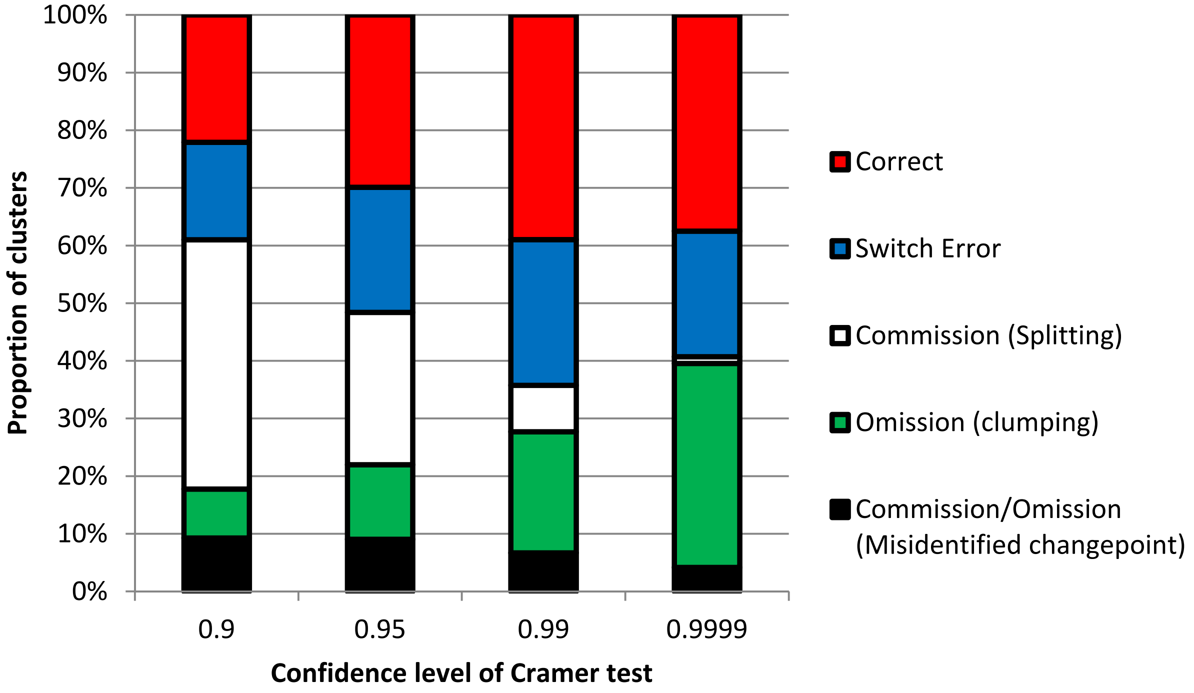


Fig 3.3 The accuracy of kernel analysis estimated utilization distribution without identifying change in individual movement phases (Full UD) and including change-point detection prior to kernel analysis (CPUD) in estimating the true movement phase distribution was high. The volume of intersection (VOI) was used to quantify the joint distribution between the true multivariate exponential power distribution used to generate the data and each estimated utilization distribution.

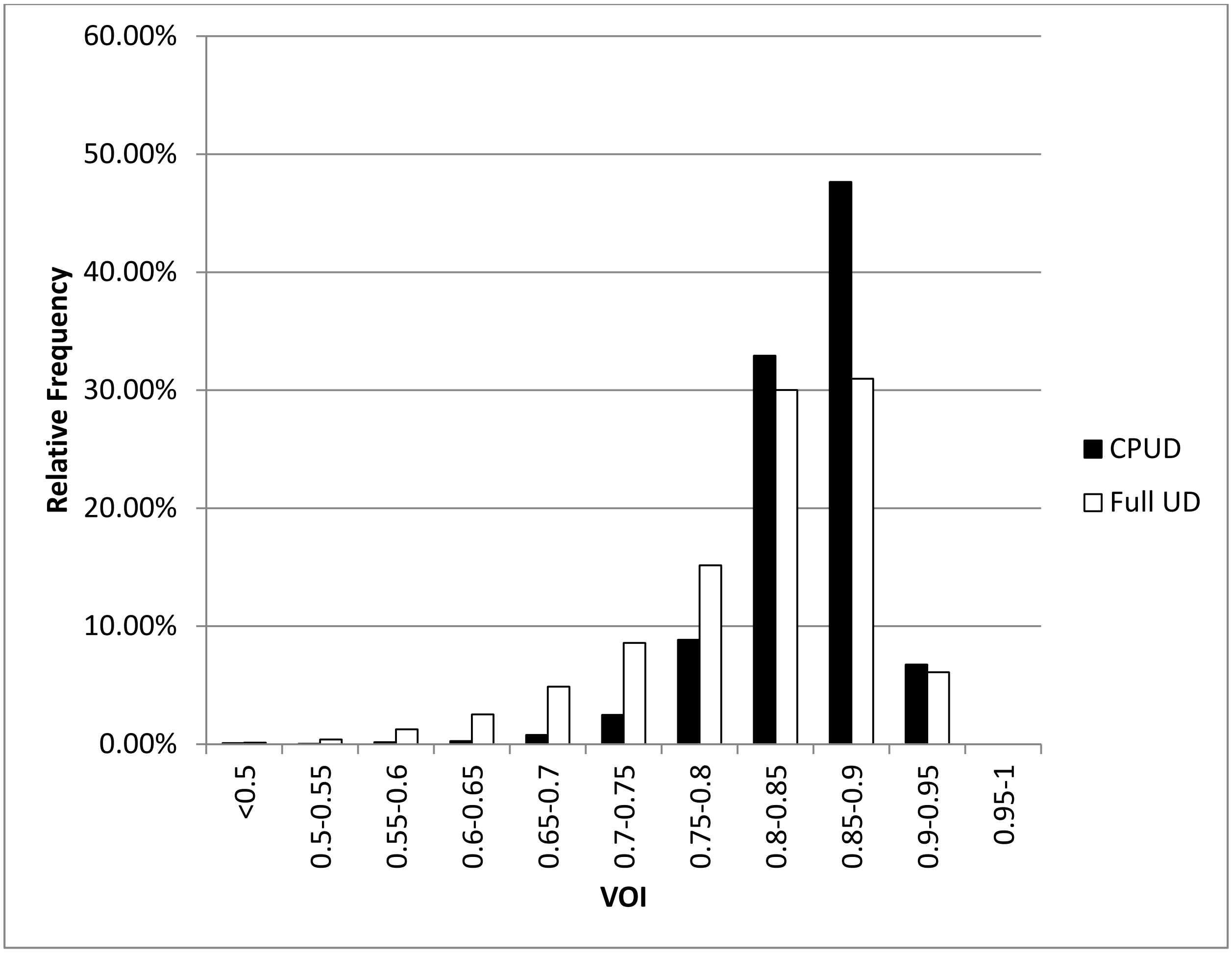


Fig 3.4 The difference in change point utilization distribution (CPUD) and full utilization distribution (Full UDs) estimates of the true movement process show increased CPUD accuracy (VOI Difference >0) even when the correct numbers of change points were not estimated.

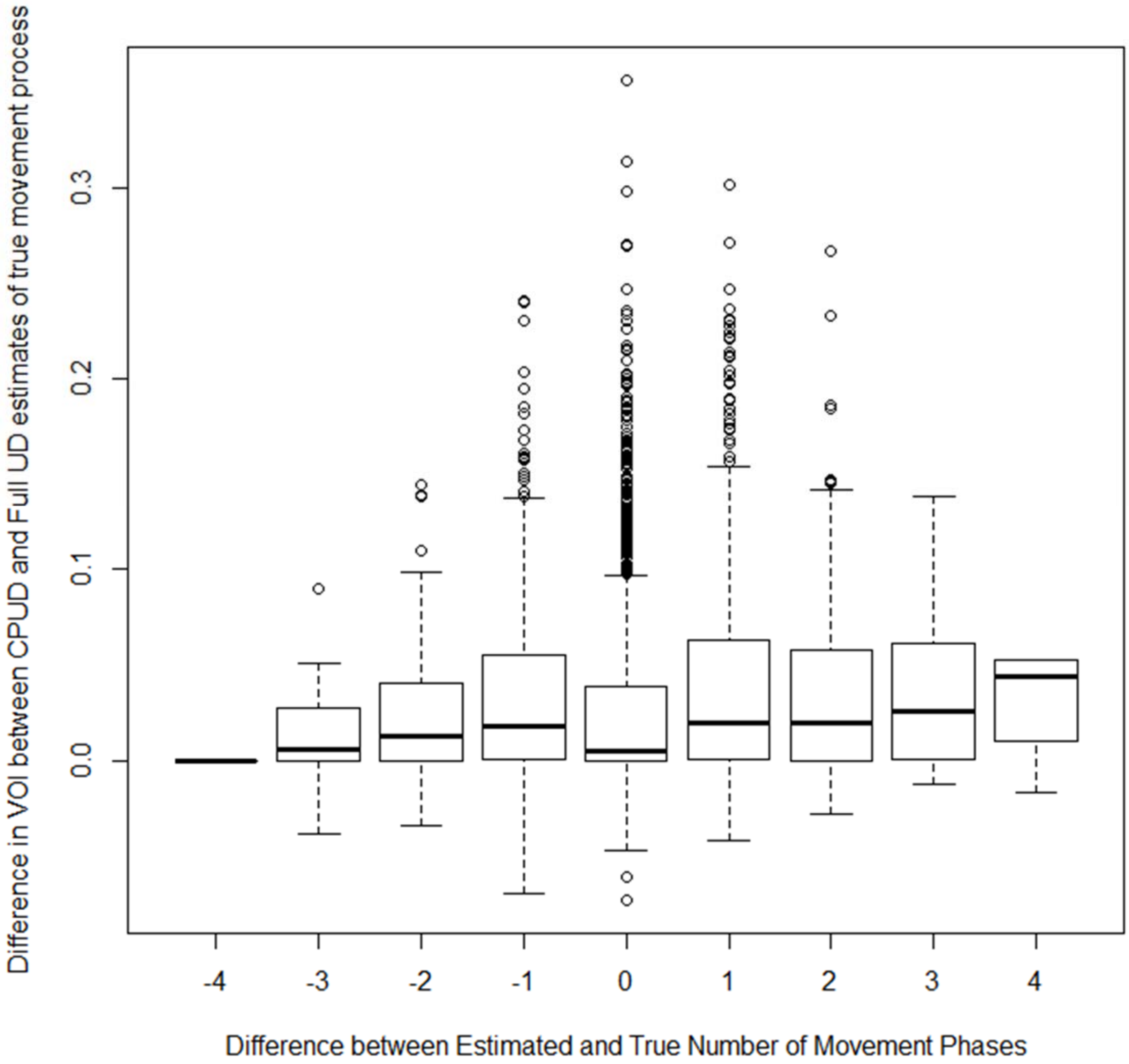


Fig 3.5 Change point estimation typically improved estimation of the movement process (positive difference in VOI) by change point utilization distributions (CPUDs). Improvements occurred both when multiple movement phases occurred (a) and when they were estimated (b) in the data. When no change points were estimated the Full utilization distribution (FULL UD) and CPUD were identical and equally estimated the movement process. Improved estimates of the movement process occurred even when more movement phases were identified than actually occurred in the data (Errors of Commission)

a) b)

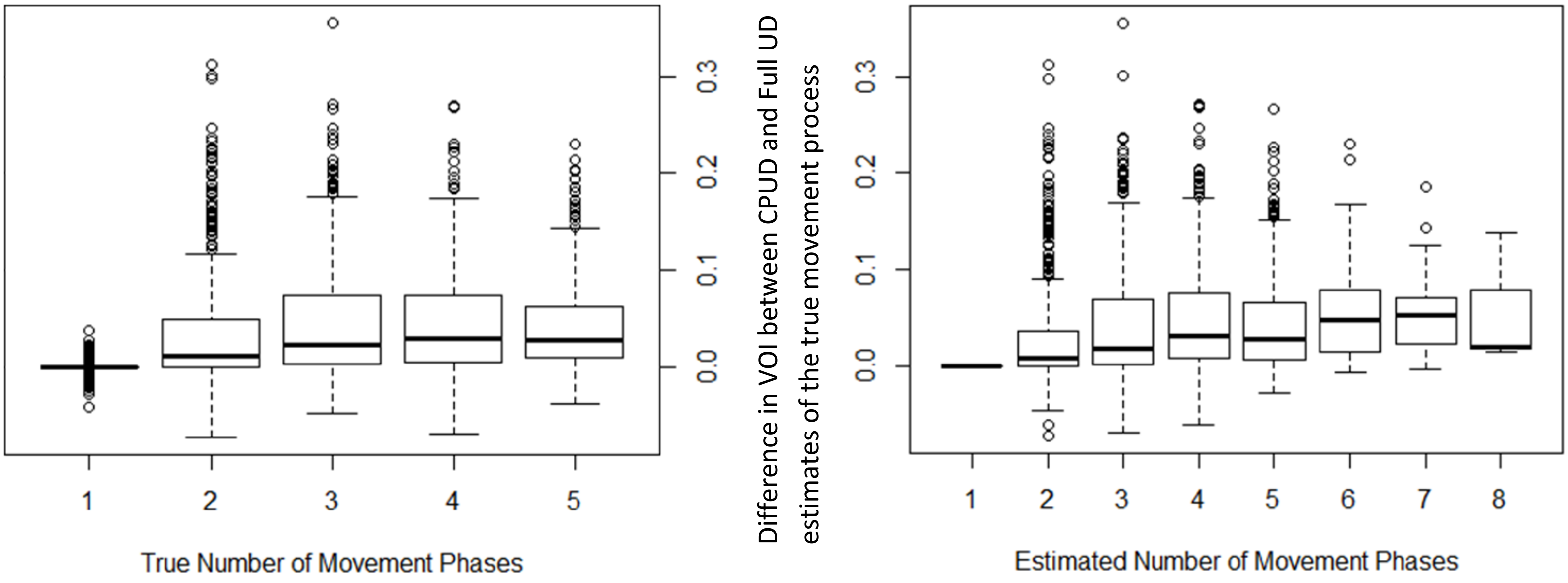


Fig 3.6 Change point detection of simulated radio-telemetry data resulted in either correct (C) identification of change point occurrence or resulted in 4 types of errors that may have biased individual movement phase estimation: error of omission (-), error of commission (+), both errors of commission and omission (-/+), and minor “switching errors” in timing of change point detection (S). Estimation of the total movement process was improved when using change point utilization distributions (CPUDs), relative to traditional kernel analysis (Full UDs), and this improvement was mostly invariant to the type of error (a), or number of errors (b) occurring

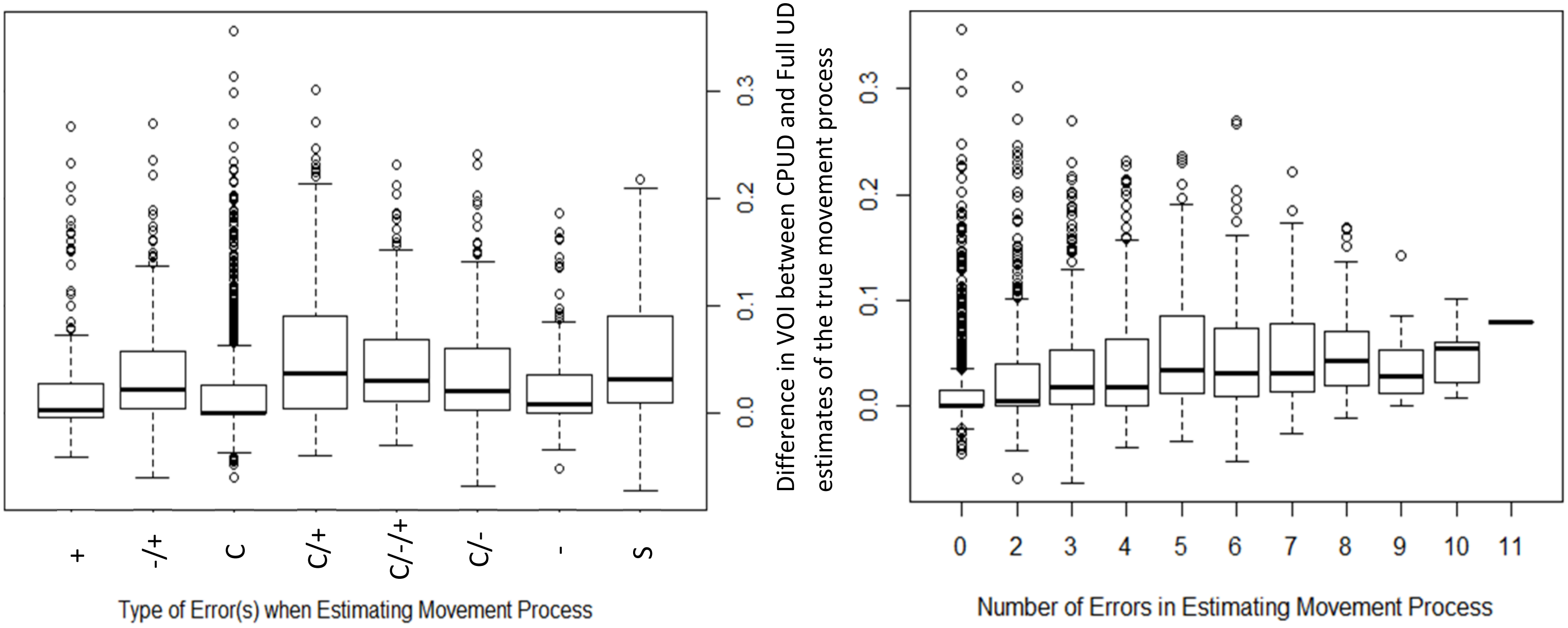


Fig 3.7 Core areas estimated by change point utilization distributions (CPUDs) often estimated different spatial regions that core areas estimate by Full utilization distributions (Full UDs), particularly when multiple movement phases were present in the data

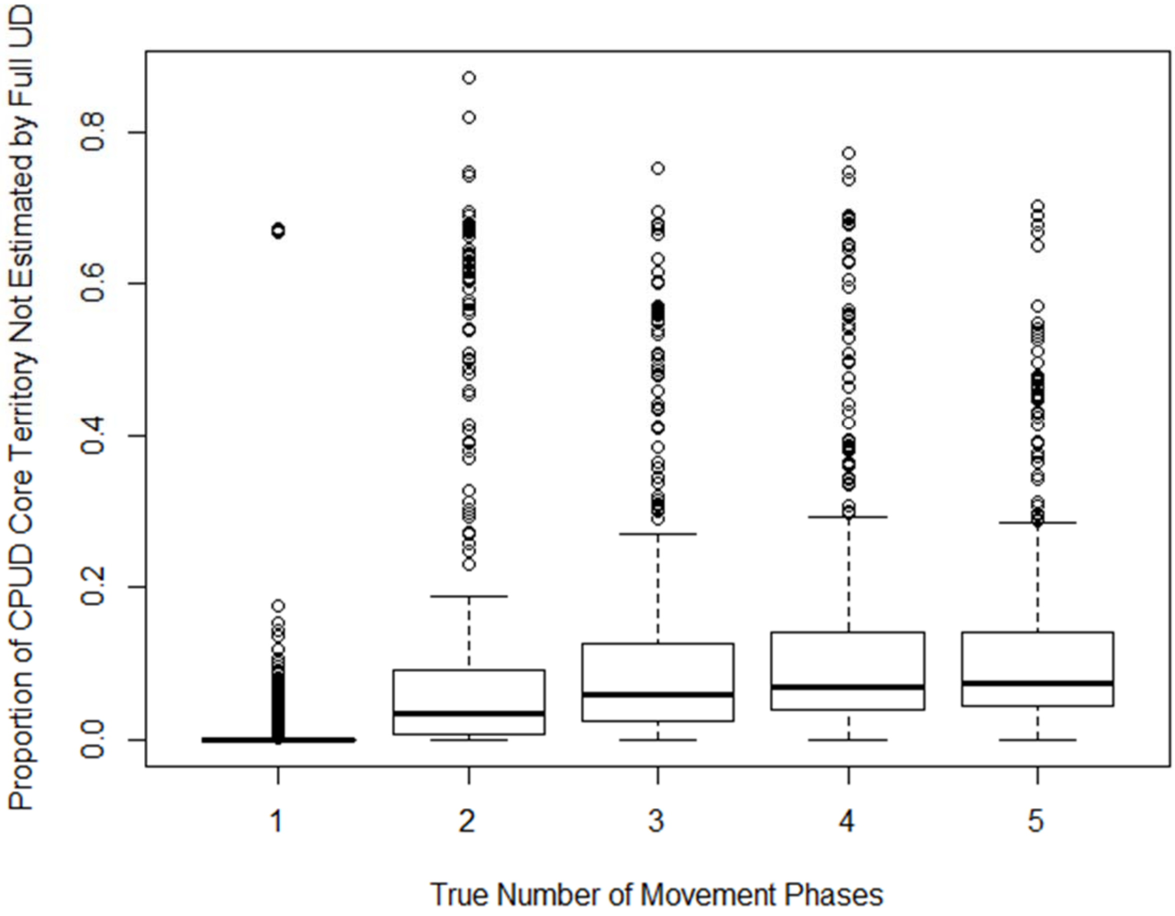


Fig 3.8 The similarity of estimated movement process between the full utilization distribution (Full UD) and the change point utilization distribution (CPUD) was estimated using the Volume of Intersection (VOI) between both space use estimates. Space use estimates were less similar when the CPUD technique was a better estimator of the movement process

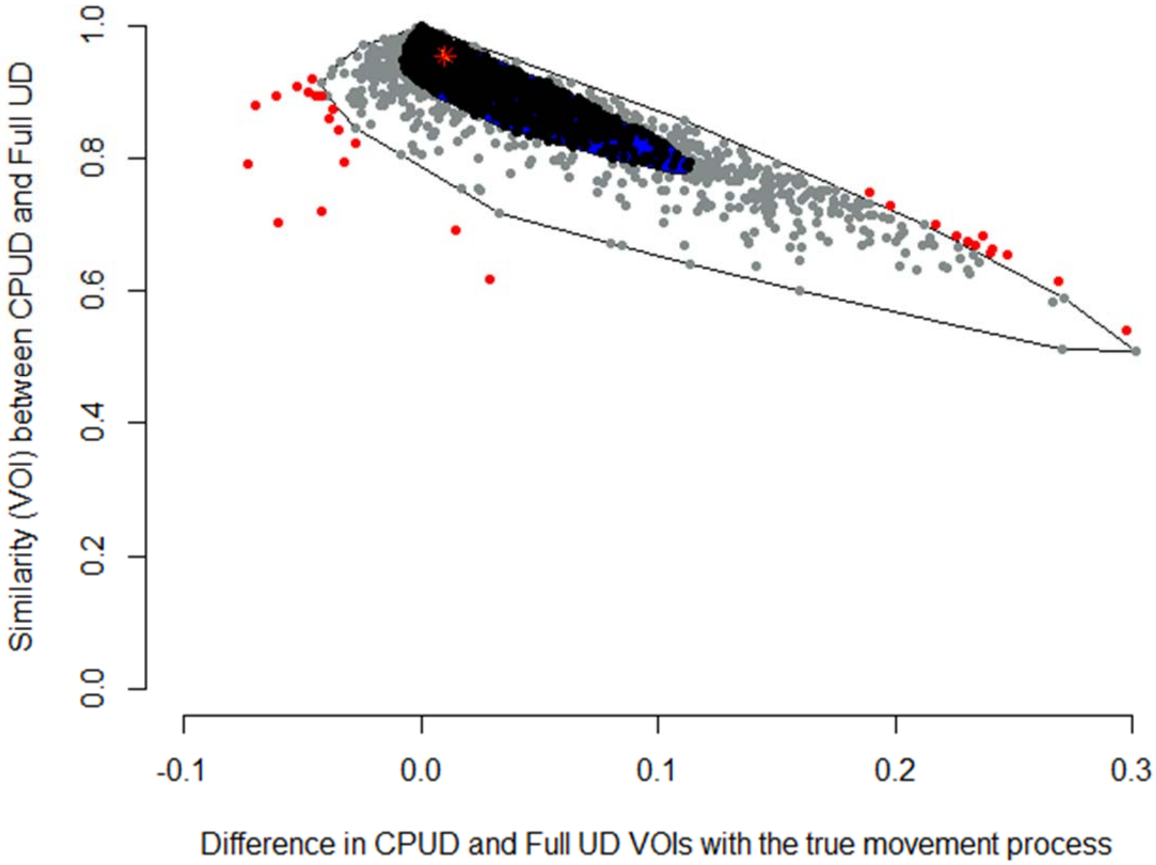


Fig 3.9 Accuracy of change-point utilization distributions (CPUD), relative to full utilization distributions (Full UD), increased when multiple movement phases occurred in the data and when the centers of movement phase distributions were further apart

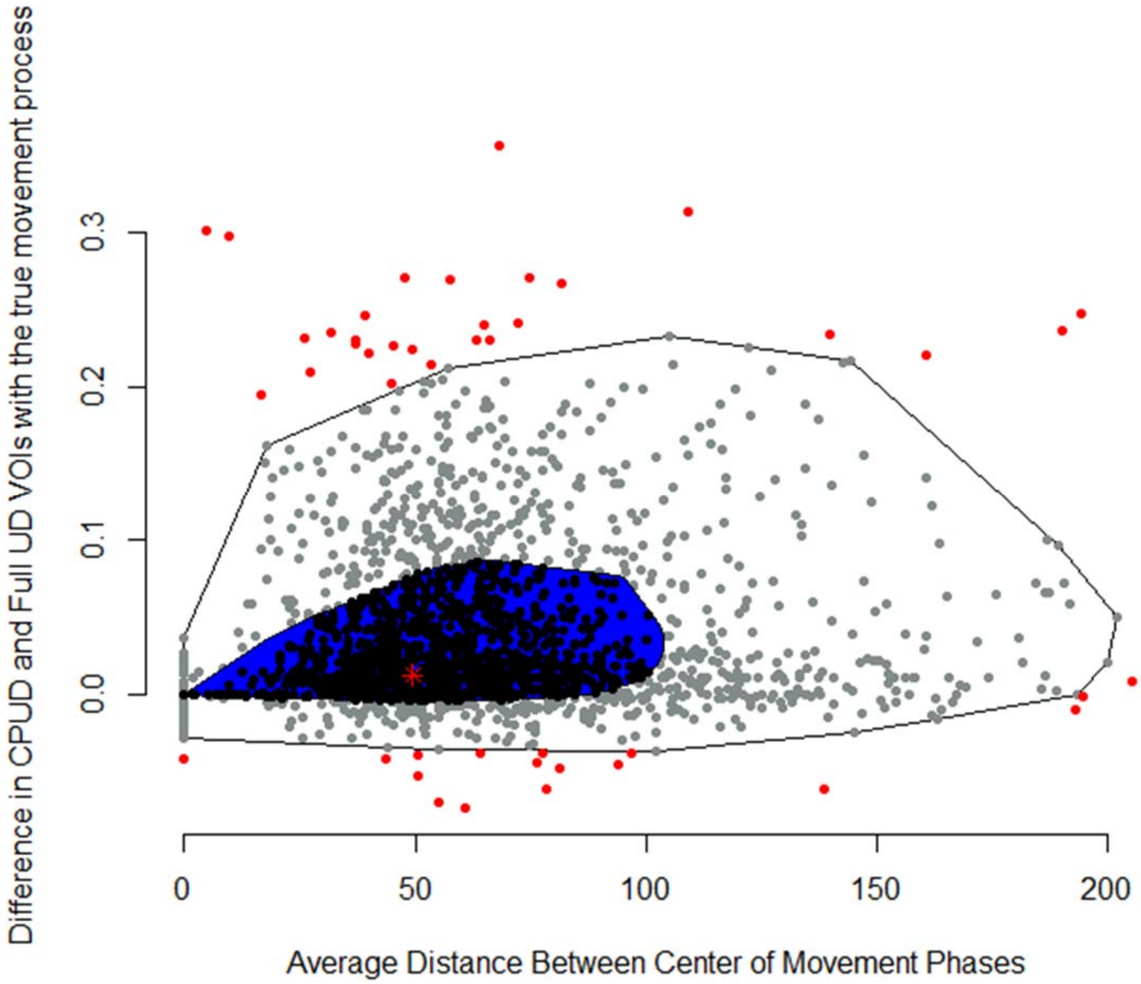


Fig 3.10 Improved space use estimation using change point utilization distributions (CPUD), relative to traditional kernel analysis (Full UD), occurred even when change-point detection resulted in few locations occurring in estimated movement phases. Individuals with no change-points estimated are removed since the CPUD and Full UD are identical

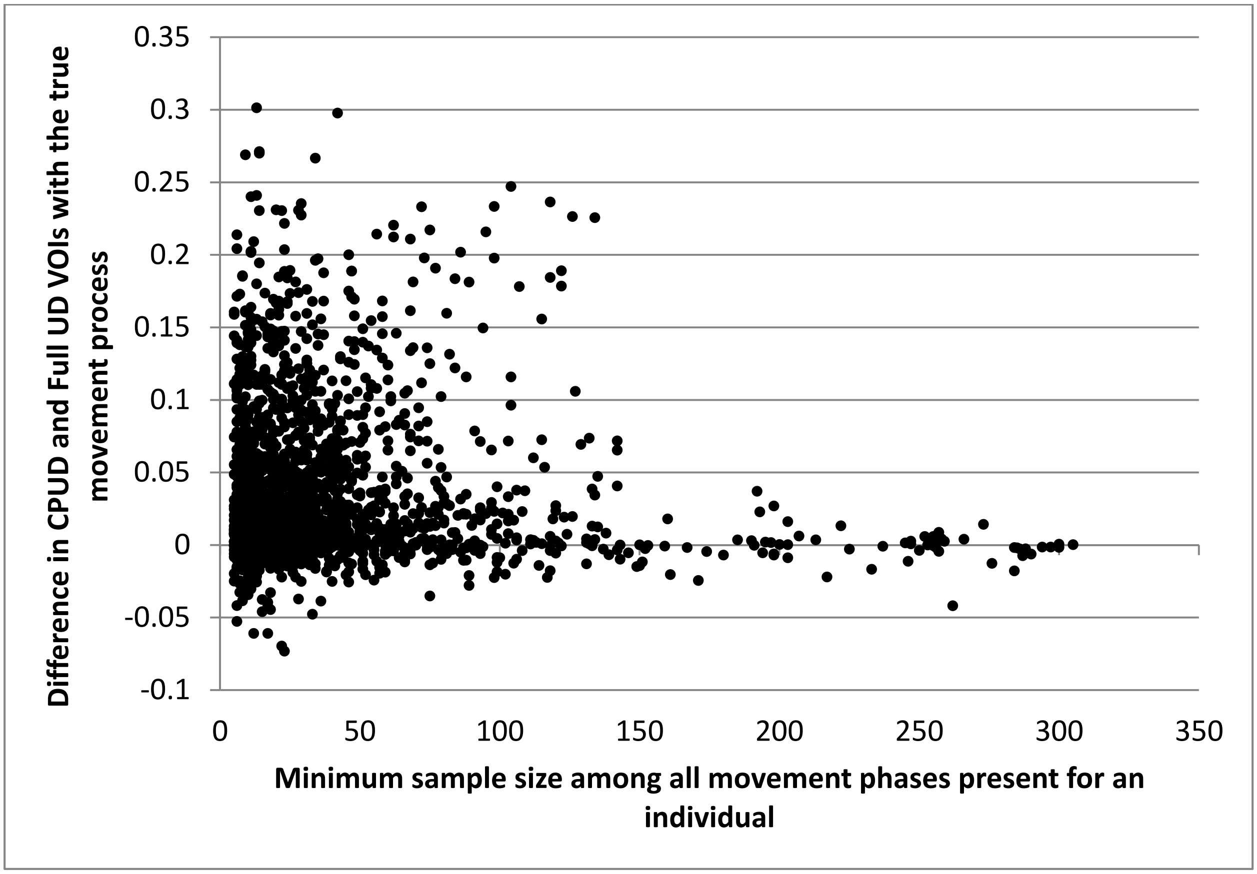
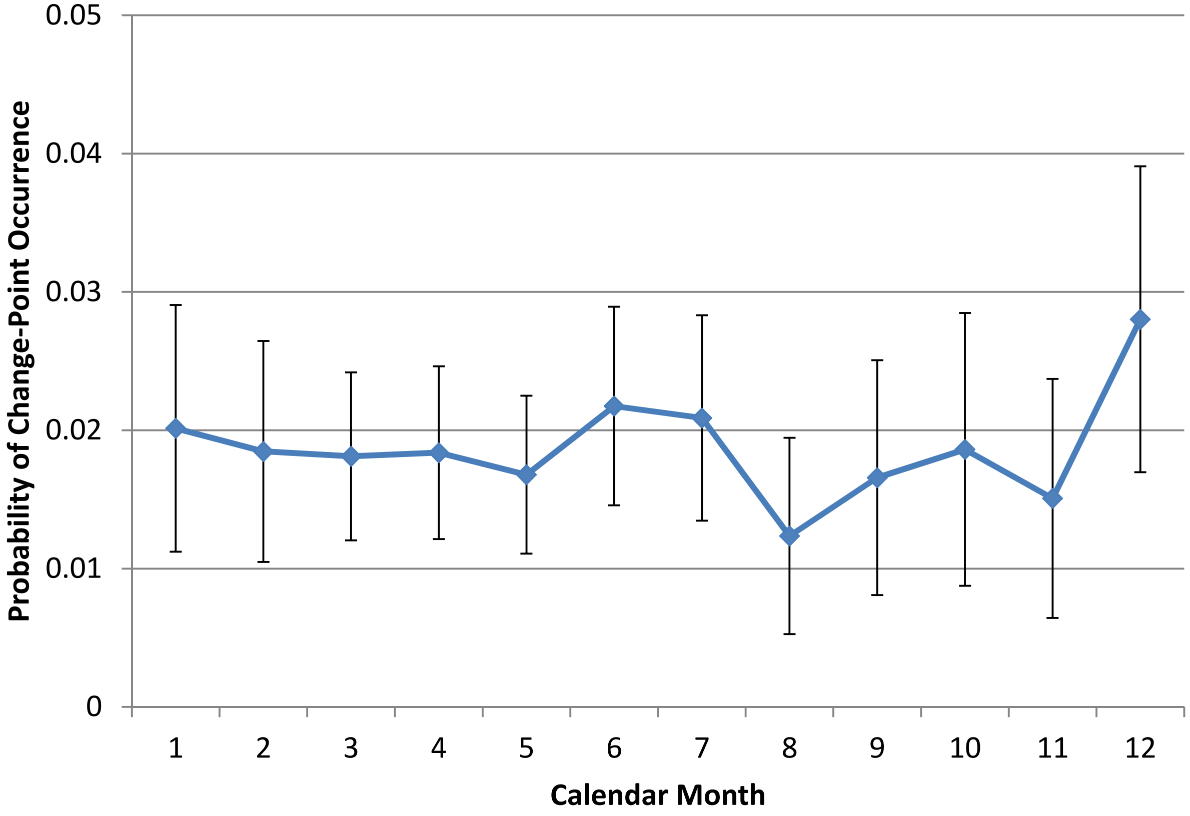


Fig 3.11 Probability of change point occurrence by month of year for 100 California clapper rails tracked between January 2007 and September 2010 in San Francisco Bay, California (n = 15,392). Error bars indicate two standard errors



CHAPTER 4: Inferring territory size of a secretive marsh bird: the endangered California clapper rail

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ABSTRACT

Territorial defense of limited resources by animals is a behavior that has important implications for population dynamics particularly for species occupying fragmented habitats. Territories are often quantified by spot mapping locations of aggressive bouts or displays. However, such methods may not work effectively for secretive species or when observations of behavior are impractical. The endangered California clapper rail (*Rallus longirostris obsoletus*) is such a species. It is known to be territorial but habitat structure, shifting patterns of space use, and habitat structure preclude accurate spot mapping of territory boundaries. We estimated space use patterns of 100 California clapper rails radio-marked in San Francisco Bay between 2007 and 2010 from homogenous point patterns. We then quantified the territory with each of these movement phases where neighboring individuals had priority access to the resources. The annual average threshold where territoriality occurred among clapper rails equaled the 49.7% isopleth of kernel density estimates and territory size averaged 1.2 ha throughout the year. During the breeding season, the average territory threshold increased to 55.5% and average territory size increased to 1.45 ha. Population density implied by these territory sizes (1.38 birds/ha) is comparable to density estimates during the 1970s and 1980s. These findings provide a baseline for expanded research into factors such as population density and resource availability that influence territory size of this secretive species as well as guidance for evaluating species management and habitat restoration actions.

INTRODUCTION

Intraspecific competition occurs when individual animals secure discrete areas with resources and preclude access to other individuals “by means of repulsion through overt defense or advertisement” (i.e. exhibit territoriality; Wilson 1975). Such intraspecific contest competition is expected to affect dynamics of the whole population (Nicholson 1954; Brannstrom and Sumpter 2005). This contest competition results in unevenly distributed resources among all individuals in a population and may result in more individuals surviving resource shortages than would occur if scramble competition occurred, wherein resources were equally distributed among individuals (Lomnicki 1980). The size of defended territories may fluctuate or remain static with resource availability leading to stable or fluctuating population densities, respectively (Adams 2001).

Quantification of territory size is often accomplished through spot mapping, observation of territorial display or aggression, and delineation of boundaries (Bibby et al. 1992). However, this is not always possible for secretive species for which behavioral observations are difficult or impractical. An alternative technique to estimate territory size quantifies territory boundaries using overlap among adjacent individuals’ home ranges. Home range overlap among territorial animals has been used in mechanistic agent-based models to quantify red fox (*Vulpes vulpes*) territory formation and expansion in populations following precipitous population declines (Potts et al. 2013). However, Potts et al. (2013) note that territories may fluctuate in size and location through time and ecological studies using kernel density estimation to quantify home range overlap may not be able to obtain sufficient locations for analysis before territorial borders change. Changes in individual movement patterns represented by non-stationary or inhomogeneous point patterns can result in significant bias in home range estimates particularly when using kernel techniques (Downs et al. 2012). However, statistical modeling suggests that change-point utilization distributions (CPUDs) can detect shifts in the mean or spread of a sequence of animal relocations and more accurately quantify space-use patterns when such changes occur (Chapter 3).

Researchers have used many different operational definitions of territoriality (Maher and Lott 1995) and home range. To facilitate future comparisons we provide an explicit distinction between three terms relevant to individual space-use: home range, movement phase, and territory. We accept Burt's (1947) definition of a home range as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young". Home ranges, therefore, are spatial representations of medium- to long-term behavior typically occurring over month or years. A movement phase is a subset of a home range that has a homogenous pattern, mean or variance, of constituent relocation coordinates (Chapter 3). Change point utilization distributions estimate movement phases and we use the terms interchangeably. Movement phases can occur over short time frames, including transitory movements that are extralimital to home range patterns, or be equivalent to a home range when the entire point pattern is homogenous and change points are not detected (Chapter 3). We adopted the definition of territorial dominance used by Kauffman (1983) wherein one individual has priority access to resources, i.e. one individual's estimates of space use exceed another's (Maher ant Lott 1995). Using this definition, when concurrently occupied movement phases overlap among adjacent individuals the territorial boundary between individuals occurs where the cumulative kernel probability density (i.e. kernel isopleth) is equal and minimized (Figure 1). We term this minimum common isopleth the "territory threshold" as it represents the region of their respective CPUDs within which each individual has priority access to resources.

The California clapper rail (*Rallus longirostris obsoletus*) is a state- and federally-listed endangered species that occupies remnant and restored tidal marshlands in San Francisco Bay. The first attempts at quantifying clapper rail population sizes occurred in the 1970's when 4,200-6,000 individuals were counted in 120 censuses on 4,778 ha of marshland. Populations of clapper rails had declined to a few hundred individuals by the early 1990's before rebounding to a few thousand by 2007 (Albertson and Evens 2000, McBroom 2012, Liu et al. 2009). However, apparent densities have largely not recovered to levels seen during the 1970's. California clapper rail annual home ranges are small and home range sizes do not vary among sexes or seasons (Rohmer 2010, Albertson 1995). The clapper rail is monogamous and both sexes defend a territory. However, the relationship between clapper rail home range size and defended territory size remains unknown.

The secretive nature of clapper rails and tall intertidal vegetation present in San Francisco Bay preclude delineation of individual territories by spot mapping. Here, we quantify territory size among radio-marked California clapper rails using overlap among CPUDs. We assessed the degree of territoriality and average territory size temporally and for two types of social interactions: mated pairs and unmated neighbors. We predict that mated pairs will have low territory thresholds indicating the lack of territoriality between mated individuals. Contradictory evidence of the seasonality in territorial defense exists. Territoriality may be reduced or suspended during the winter and periods of extreme tidal inundation, but presumed mated pairs defended artificial tidal refuge habitats in San Francisco Bay during the winter (Chapter 2; Rush et al. 2012; Zembal et al. 1989). Therefore, we predict that the territory threshold among adjacent individuals will be greatest and territory size will be smallest during the breeding season. Territory size has not been estimated for California clapper rail, but average territory sizes estimated by spot mapping locations of calling Yuma clapper rails (*R. l. yumanensis*) was 1.4 ha (Smith 1974). We predict California clapper rail population sizes will be comparable. Lastly, we inferred population density from the territory sizes we observed to provide baseline information for species conservation and habitat restoration goals as well as future ecology studies on the role population density and resource availability have in influencing individual spacing (Adams 2001).

METHODS

We analyzed radio-telemetry data from 100 California clapper rails (15,392 locations) obtained between January 2007 and September 2010 using change point utilization distributions (Chapter 3). This change point detection and resultant kernel analysis quantified homogenous point patterns within the sequence of radio-telemetry relocations among all individuals using the nonparametric and multivariate Craemer test (Chapter 3). Since territoriality between neighbors can only be evaluated when space use is both concurrent and overlaps occurs, all combinations of paired movement phases (127,092 potential pairs; n!/(n-2)!, n=357) were limited to only movement phases which were in use by birds at the same time. Furthermore, we used the PHR overlap metric (Fieberg and Kochanny 2005) to identify concurrently occupied movement phases where 5% or more of an individual's CPUD occurred within the 95% isopleth of another CPUD bird. These two factors ensured that we evaluated territoriality only among neighboring individuals with concurrent estimates of their respective space use. We identified the type of social interaction (mated pair or unmated neighbors) represented by the overlapping CPUDs based on nesting activity, if observed, or proximity and sex identification during capture if breeding activity was not observed.

We calculated the territory threshold, the point within paired-movement phases wherein each individual had priority access to available resources, among all concurrently overlapping CPUDs and estimated the territory sizes for both individuals. Since movement phases changed frequently (Chapter 3), we summarized the average territory threshold and average territory size daily among all pairs of individuals for which overlap occurred. We then tested for differences in the daily average territory threshold, and for daily average territory size, between mated and unmated individuals and tested for differences within each group by month of year using nonparametric Kruskal-tests adjusted for multiple comparisons (Siegel and Castellan 1988). Large movement phases could have overlapped multiple other birds and resulted in non-independence among samples. Therefore, we tested if CPUD size was related to the observed territory threshold using Pearson's correlation test. Significant correlation between CPUD size and territory threshold would indicate estimates of territoriality (territory threshold) are dependent on the size of the overlapping space use estimates. The inverse of territory size provided a measure of the space used predominantly by an individual, which we interpreted as the observed population density given territorial behavior. We note that not all individuals within the population were radio-marked and the observed territory threshold may underrepresent the maximum extent to which CPUDs of neighboring individuals overlapped resulting in larger territory sizes and smaller population density estimates.

RESULTS

We estimated California clapper rail space use using CPUDs, which resulted in 357 movement phases and included 1 to 13 movement phases per individual. All possible combinations of CPUDs (127,092 pairs) were evaluated for concurrent use resulting in 2,110 movement phase combinations where overlap among pairs occurred on at least one day of use. Among these, 1,551 paired CPUDs were spatially isolated from each other (<5% overlap among UDs) resulting in 582 (mated pairs = 31; unmated neighbors = 551) movement phase pairs used in subsequent analyses. Only five individual clapper rails had movement phases that never overlapped those of other radio-marked birds and 294 (82%) of all movement phases overlapped at least one other movement phase. The average time that overlap among CPUDs occurred was 35 days (range: 1-442 days).

We quantified territorial behavior among unmated California clapper rails with the average daily territory threshold, the point between individuals' cumulative kernel density that indicated priority access to resources (i.e. minimum common isopleth among CPUDs). The average daily territory threshold among unmated individuals was 49.7% (range: 4.8% to 85.6%) across the entire year, but increased during the peak of the breeding season (April to July) to 55.5% (range: 31.6% to 84.2%). The distribution of territory thresholds among unmated clapper rails differed by month of year and was lowest following the breeding season (Figure 2). In contrast, evidence of territoriality between mated individuals was low particularly during the peak of the breeding season (April-July). The average daily territory threshold, the point within mated individuals' cumulative kernel density that indicated priority access to resources, was 6.7% (range: 0.6% to 26.8%) across the year. The distribution of territory thresholds between mated pairs differed by month of year with higher territory thresholds occurring primarily during the winter (Figure 2). The size of CPUDs were not significantly correlated with the estimated territory thresholds (Pearson's r = -0.004; p = 0.89) which suggests our data were independent.

The average daily size of territories implied by our estimates of the territory threshold between unmated California clapper rails was 1.2 ha (range: 0.04 to 3.03 ha). Pairwise-Kruskal tests indicated the distribution of average daily territory size differed among months and was slightly larger during the breeding season and smaller following the breeding season (Figure 3). Median territory size ranged from 0.93 ha in December to 1.45 ha in June and greater variation in estimated territory size was observed during the winter. Since mated clapper rails are not territorial against their mates, territory size indicates the amount of space used predominately by a pair of birds and the inverse of territory size provides a measure of population density. On average, annual California clapper rail density was 1.62 birds per hectare among occupied territories in San Francisco Bay between 2007 and 2010. During the breeding season when territories were larger (1.45 ha), estimates of the average density dropped to 1.38 birds per hectare.

DISCUSSION

We used overlap among concurrent change-point utilization distributions from neighboring California clapper rails to quantify the threshold at which each individual has priority access to resources. Our findings agree with the generally accepted description that clapper rails are territorial during the breeding season and the degree of territoriality is reduced following the breeding season when juveniles become independent (Zembel et al. 1989). Our results are the first to quantify territory size for this subspecies and are comparable to nesting territory estimates of Yuma clapper rails (*R. l. yumanensis*; 0.12-3.59/ha) along the Colorado River (Bennett and Ohmart 1978). Furthermore, the population density implied by our average territory size is similar to historical estimates (0.3-1.6 birds/ha; Gill 1979 and 0.69-1.59 birds/ha; Harvey 1988) in San Francisco Bay and larger than estimates when population size was lowest in the early 1990s (0-1.71 birds/ha; Albertson 1995 and 0.18-0.64 birds/ha; Foerster et al. 1990).

Territorial behavior is a crucial aspect of a species' ecology that influences species distributions, fitness, and resilience to environmental change by creating a density dependent regulating mechanism (Newton 1998). Understanding this mechanism is therefore, of crucial importance when managing endangered species in fragmented habitats. Under simplifying assumptions, territory size can be extrapolated to derive an equilibrium population size or carrying capacity without non-breeding "floaters", or effective breeding population size if floaters are present (Lopez-Sepulcre and Kokko 2005). Estimates of California clapper rail carrying capacity would greatly enhance monitoring of population recovery goals

(USFWS 2010) and evaluating tidal marsh restoration projects (Trulio et al. 2007). However, carrying capacity is a function of total resource availability, individual resource needs, and how individuals compete for resources, all of which may vary over time (Ayllon et al. 2012). Furthermore, space use patterns are rarely a simple tradeoff between resource benefit and defense costs. Traditional density dependent mechanisms such as territory establishment by floaters, intrusion by neighbors, and territory expansion are all possible factors influencing space use of California clapper rails. However, density independent factors such as breeding status, environmental triggers, and death of a bird's mate have also been identified as potential factors influencing how clapper rails use space (Chapter 3). Radio-telemetry is a common method for estimating space use patterns, particularly an individual's home range (Millspaugh and Marzluff 2001). However, the relationship between home range and defended territory is not well understood for most species and may be substantially different (Anich et al. 2009). Additionally, space use patterns may not be constant for extended periods of time (Fryxell et al. 2008). Multiple movement phases within locational data result in biased estimation of space use patterns using traditional (e.g. kernel density) approaches (Downs et al. 2012) unless change-points in location distributions are identified first (Chapter 3).

Understanding territoriality in the endangered California clapper rail is important because populations that exhibit territoriality often have lower abundances than non-territorial populations (Lopez-Sepulcre and Kokko 2005), which increase the risk of local extinction. Variation in territory size as a response to ecological conditions (e.g. food abundance or population density) may also influence population dynamics (Adams 2001). Territory sizes observed among neighboring clapper rails in San Francisco Bay were relatively stable throughout the year despite seasonal variation in both the overall size of spaces used (movement phases) and the threshold within which territorial space use was evident. It remains to be seen whether territory size fluctuate with population density or with the amount of resources (e.g.

food, tidal refuge) available. Any such relationship that results in fluctuating territory sizes could indicate increased extinction risks to clapper rail populations, which often have low absolute abundances and occupy a narrow ecological niche (Vucetich et al. 2000; Harnik et al. 2012).

It is important to note that survey methods to index California clapper rail population sizes rely on detections of calling individuals (Liu et al. 2009, McBroom 2012) which do not necessarily reflect the number of breeding pairs. Non-breeding individuals that do not maintain territories (i.e. “floaters”) may occur in larger populations or because of demographic stochasticity in smaller populations and they can provide an additional buffer to population fluctuations (Lopez-Sepulcre and Kokko 2005). The presence of floaters can explain Alee effects and the greater population densities observed in larger habitat patches (Penteriani et al. 2008). California clapper rail population density has been found to vary positively with marsh area (Evens and Collins 1992). Positive relationships between population density and patch area may be the result of Allee effects (Berec et al. 2007) and/or a consequence of autecological process such as negative edge effects or increased emigration rates (Bowman et al. 2002).

Additional research is needed on the reasons for territoriality in California clapper rails if population recovery goals are to be met and effectiveness of habitat restoration to be evaluated. Numerous authors have reported on clapper rail territorial behavior during the breeding season (Zembal et al. 1989; Meanley 1985; Albertson 1995). A focus on breeding season territoriality is perhaps warranted since competition for nesting territories is a suggested method of regulation in Atlantic Coast clapper rail populations (Ferringo 1966; Widjeskog 1974 as cited in Gill 1979). However, we don’t expect that the slightly larger territory size among clapper rails during the breeding season (1.45 ha), relative to the average territory size throughout the year (1.2 ha), is sufficient evidence that breeding season territoriality alone limits California clapper rail populations given that individual survival rates are lower and selection of artificial tidal refuge habitats is greater during the winter. The periodic tidal inundation of the primary forage habitats used by clapper rails in San Francisco Bay (i.e. 2nd and 3rd order tidal channels; Garcia 1995) may result in territorial behavior exhibited in much the same manner that territoriality is demonstrated by pied wagtails (*Motacilla alba*; Davies and Houston 1981). Pied wagtails defend territories along river systems that are large enough for food to be replenished from upstream during the time it takes to forage from one end of the territory to the other. Clapper rails are routinely seen foraging for mollusks and other prey at low tides along channels. Foraging opportunities or capture success rates may decrease with the time as benthic invertebrates burrow deeper into substrates. Clapper rail territory sizes must be large enough to ensure sufficient forage is captured while the tide is out.

Future research should investigate whether territory sizes are either resource (e.g. food availability) or population density driven. However, experimental manipulation of food resources or population sizes is not likely for this endangered species and behavioral observations of focal animals are not feasible. Therefore, information gained on territoriality will probably be restricted to inferences from neighboring individuals' space use patterns and reliance on "natural experiments" such as environmentally driven population crashes and incremental change in habitat conditions resulting from habitat restoration.

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FIGURES

Fig 4.1 Conceptual model for quantifying territory size from overlapping home ranges. The minimum isopleth common to two individuals quantifies the territory threshold, the point of each utilization distribution wherein each individual has priority access to resources.

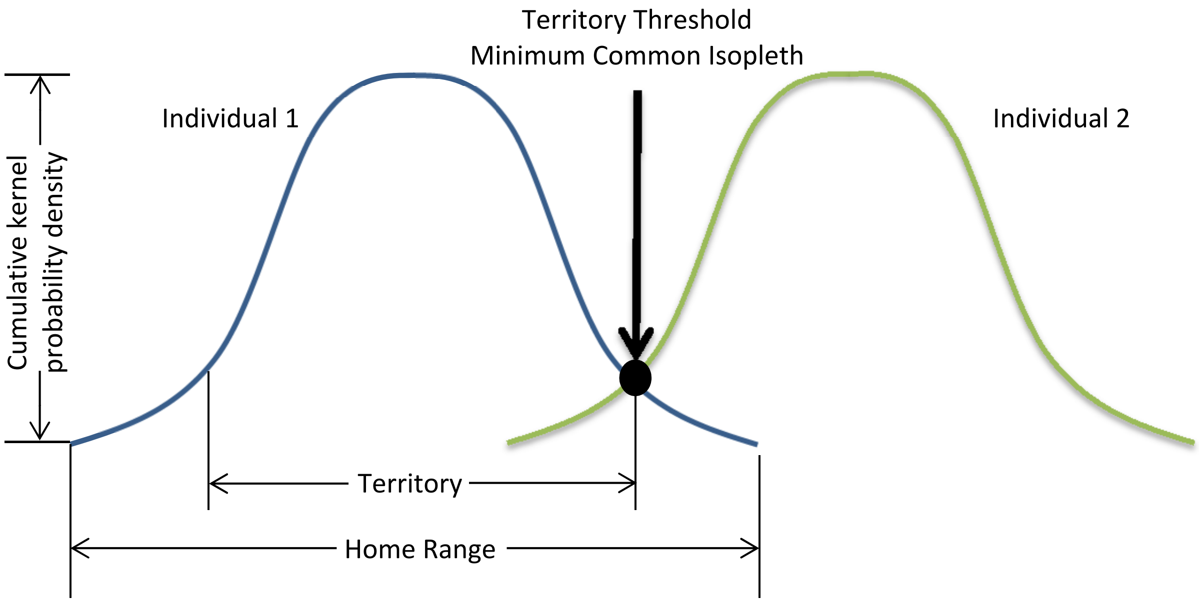


Fig 4.2 Average daily territory threshold by month among mated (blue) and unmated (red) California clapper rails in San Francisco Bay 2007-2010. Territory thresholds between unmated birds were greater than mated birds in all months. Months with the same symbol were not significantly different from each other (Kruskal-test; p>0.05)

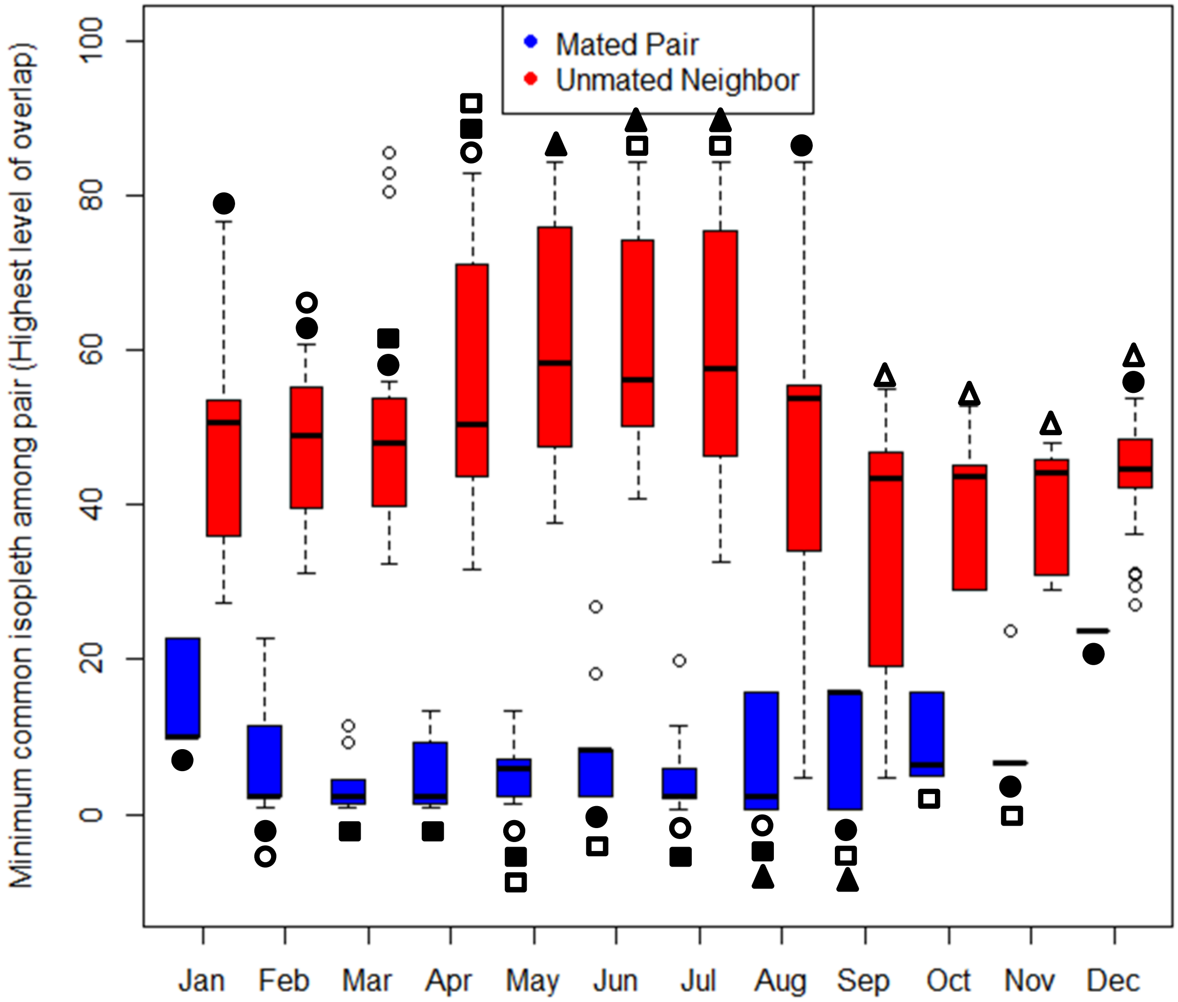
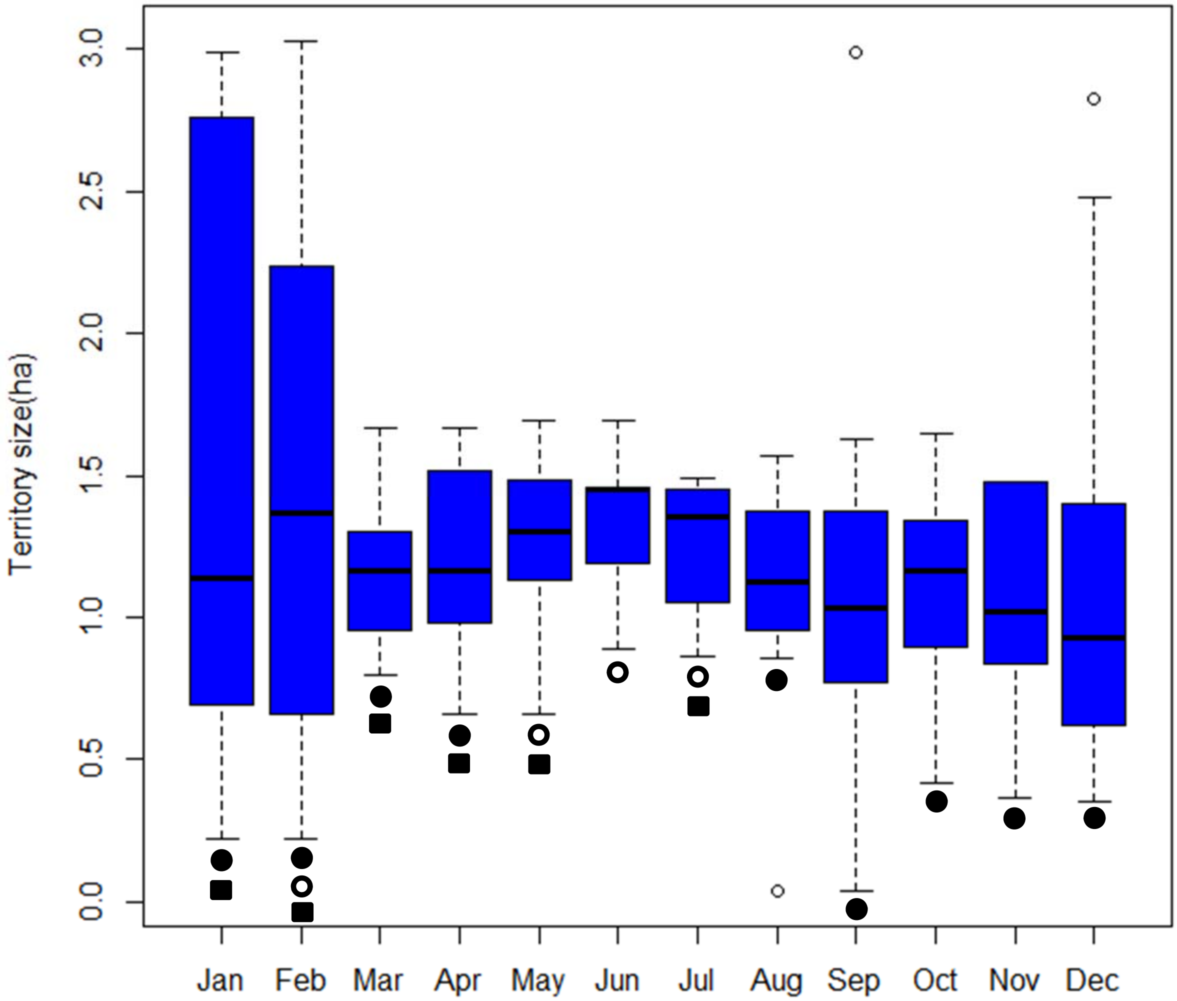


Fig 4.3 Average territory size for California clapper rails whose space use overlapped that of neighboring rails in San Francisco Bay, 2007-2010. Months with the same symbol were not significantly different from each other (Kruskal-test; p>0.05)



SUMMARY

Influence of tides on California clapper rail ecology

This research has shown that tides exert a strong influence on many aspects of California clapper rail ecology. From demographic processes to habitat selection, tidal inundation creates limits that are intrinsic to life in San Francisco Bay saltmarshes and to which clapper rails must respond. Tidal inundation operates as a density independent factor effectively reducing the amount or quality of habitat available for clapper rails relative to low tide conditions. Habitats that are immune to tidal inundation, such as the artificial floating islands investigated in Chapter 2, increase in importance to clapper rails as tide heights increase as shown by the increased use observed once tides started covering the marsh surface. This type of abiotic forcing may increase the severity of density dependent factors that influence survival if tidal refuge becomes sufficiently limited during extreme high tides. In Chapter 1, I showed that tide height correlated with lower survival rates in California clapper rail populations. While the data available were not sufficient to examine density dependent factors influencing survival, they are worth mentioning for two reasons. Firstly, maximum population abundance in a salt marsh may be determined by the amount of tidal refuge available and not the size of the marsh itself. This suggests that habitat enhancements that provide additional tidal refuge cover, for instance adding “islands” of high ground or encouraging taller vegetative structure, may be particularly effective in lower marshes that are topographically homogenous and have relatively low population density. A second reason to consider tidally accentuated density dependence is that tide heights, and perhaps more importantly tide ranges, have been increasing in San Francisco Bay for the last 100 years (Cayan et al. 2008) and are projected to increase dramatically in the future (National Research Council 2012). Populations that appear stable now may soon experience reductions in suitable refuge habitat leading to population declines. There is some evidence that the current effort to remove Invasive Spartina has resulted in similar patterns since marshes that once had among the highest clapper rail population densities were reduced to lower but often stable densities (Liu et al. 2009).

Periodic reduction in the amount of refuge habitat due to tidal inundation may not promulgate increased density dependence if clapper rails relax territorial behavior during high tides or during the winter when much of the tall monocot vegetation that provides refuge cover (i.e. *Spartina* sp.) senesces. Such behavioral plasticity regarding territoriality has been reported for clapper rails (Eddleman and Conway 1998). On one hand, I showed in Chapter 4 that territorial behavior between adjacent unmated clapper rails was relaxed during the winter. However, the space used by these rails also increased during the winter, and the relaxation in territorial behavior did not result in smaller territory sizes. Extremely high tidal inundation also occurred during many instances where clapper rails shifted their space use patterns (Chapter 3). While I could not test whether these shifts were directly related to the amount of refuge habitat available to the individual, the result of a change in the space used by an individual implies that other individuals would change space use patterns to maintain territorial boundaries. Indeed, even with the limited occurrence of adjacent clapper rails, displacement by invading individuals was observed. I posit that the dispersion of suitable refuge habitat may also be important in determining the number of clapper rails that a marsh could support. If all refuge habitats were contained in a single bird's territory and territoriality did not decrease during periods of tidal inundation, then only one bird (or presumably a pair) would be able to occupy the marsh. Such a situation may also predispose the pair to predation since there is only one patch of habitat for predators to search.

Current California clapper rail ecological conditions in relation to historic conditions

The challenges that tidal inundation pose for clapper rail are not new. However, the portion of the rail population that has to deal with these effects may have increased due to changes in the San Francisco Bay landscape over the past 150 years. Market hunting and egg collection prior to the 20th century reduced rail populations as large tracks of marshland were converted to other uses (Grinnell et al. 1918; Taylor 1894). The resulting fragmentation of these historic marshes may have concentrated rails closer to the Bay where they ultimately were surrounded by unsuitable habitats. Levees built during development of former marshland are maintained to protect the new infrastructure and do provide habitat for California clapper rails and can provide escape cover during high tides. Levees also provide access to the marshlands for terrestrial predators such as the red fox (*Vulpes vulpes*) which prey on clapper rails and are the target of an extensive control program (Foin et al. 1997; Harding et al. 2001). While this type of edge effect may have always been present, the interior of marshlands are much reduced and edge effects may be more prevalent now. Coupled these with non-native and anthropogenically subsidized predators, like red fox and Norway rat (*Rattus norvegicus*), and it becomes apparent that over a century and a half of incremental changes to the San Francisco Bay ecosystem have increased the precariousness of Clapper rail populations.

The continued and accelerating risk to clapper rail populations is likely to be accentuated if climate change effects occur as predicted (National Research Council 2012). The predicted marshland loss in San Francisco Bay during the next century will further reduce California clapper rail populations and is likely to restrict existing birds into even fewer habitat fragments (Takekawa et al. 2013). These types of changes predispose clapper rails to extinction due to environmental and demographic stochasticity and catastrophes such as oil spills, tsunamis, and earthquakes.

Recommendations for California clapper rail and habitat management

The California clapper rail is not a species doomed to extinction even under the more dire climate change scenarios. Extensive work is being done to restore tidal marsh habitats and reduce the impact that non-native and anthropogenically subsidized predators have on clapper rails (ISP 2012, US Fish and Wildlife Service 2010, Trulio et al. 2007). These efforts should continue and where possible be expanded to include regions where marshes can “migrate” as sea-levels increase. Restoration projects that include heterogeneity in the vertical structure of marshland vegetation, through either vegetation composition or ground elevation, are likely to provide suitable clapper rail habitat for a greater number of rails. However, such actions should attempt to minimize the access or occupancy of predators. Large marshes typically have greater clapper rail density than small marshes; though this is not universally true (Evens and Collins 1992). Returning land to tidal marsh by breaching levees is not the only way to increase the suitability of habitat for clapper rails, though this may improve connectivity of populations and overall resilience for the species (Fahrig and Merriam 1985).

Enhancement of existing marshland to restore or mimic historic heterogeneity may improve clapper rail carrying capacity for individual marshes where refuge habitats are limiting. Two types of marsh may currently exhibit this type of limitation: low elevation marshes that may have abundant *Spartina* but lack tidal refuge cover particularly during winter high tides; and mid elevation marshes dominated by pickleweed (particularly when lacking taller gumplant), which typically lacks sufficient height to provide refuge cover during extreme tides. The former class is relatively uncommon in San Francisco Bay and may be best exemplified by Arrowhead Marsh in Oakland. Few other examples currently exist, but as marsh vegetation composition changes due to sea-level-rise, more marshes throughout the bay may exhibit this pattern. The second category is much more common, Muzzi Marsh, Cogswell Marsh, Whale’s Tall Marsh are just a few examples where pickleweed dominates the vegetation composition.

Recent habitat enhancements by the Invasive Spartina Project (e.g. Cogswell and Whale's Tail Marshes) and Save the Bay (e.g. Arrowhead) to restore native species and vertical complexity to these marshes hold great promise to improve the situation for clapper rails in these areas. This work should be supported and be replicated elsewhere in marshes that lack vegetation diversity.

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