Reproductive and Migration Ecology of Breeding and Wintering Northern Harriers (Circus hudsonius) in Suisun Marsh, California

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Reproductive and Migration Ecology of Breeding and Wintering Northern Harriers (*Circus hudsonius*) in Suisun Marsh, California

By

SHANNON MARIE SKALOS
DISSERTATION

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Approved:

Joshua M. Hull, Chair

Marcel Holyoak

Brian J. Halstead

Committee in Charge

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Once upon a time, this Ph.D. was for me

Now, it’s for my children

Acknowledgements

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Abstract

Management and conservation plans often lack adequate data about population estimates, habitat selection, reproductive ecology, and even migration ecology of migratory species. Migratory and understudied birds, like Northern Harriers (*Circus hudsonius*), are no exception. The Northern Harrier is a widespread but declining North American raptor species that specializes in wetland and grassland habitats. They are a secretive raptor species with a unique combination of behavioral adaptations, like ground nesting, avoidance of urban development and human disturbance, and avoidance of traditional raptor trapping techniques, that make them challenging to study. Recent advances in technology, like the miniaturization of GPS/GSM transmitters, can greatly improve management and conservation of Northern Harriers and help fill knowledge gaps about their ecology and behavior across their range.

The first challenge to studying Northern Harriers was finding efficient trapping techniques to capture an adequate sample size of individuals for transmitter deployment. In Chapter 1, we developed modified and novel trapping techniques for wintering and breeding Northern Harriers. First, we reviewed and tested successful trapping techniques from other Northern Harrier breeding populations. The most widely used technique in other populations was the use of a live or taxidermy mounted owl near a nest surrounded by mistnets or dho-gazas, which facilitates capture by eliciting an aggressive response by the breeding pair. Surprisingly, none of the published techniques were successful in our population, leading to the development of a new technique. We had the highest success flushing adult females into two dho-gazas placed in a "V" formation around the nest, a method that was modified from capturing nesting American Bitterns (*Botaurus lentiginosus*). Most females did not show behavioral responses to net placement at the nest and continued provisioning nestlings without visible stress or alarm

calling. Unlike the use of an owl lure, our technique allows for passive capture with minimal disturbance to nesting birds. However, because this technique does not elicit an aggressive response, adult males are not amenable to capture with this technique. Winter trapping is typically not attempted for Northern Harriers because they rarely respond to traditional methods like bal-chatri traps baited with live lure birds or small mammals. Noose carpets can work well, but also result in incidental capture of multiple birds or different raptor species simultaneously, leading to potential injuries of captured birds. Knowing that Northern Harriers are scavengers of dead waterbirds in winter wetland habitats, we used remote-triggered bow nets baited with waterbird carcasses to capture wintering birds. This novel trapping technique was overwhelmingly successful, with nearly 80 individual birds captured across three winter trapping seasons. This technique also allows for targeted capture of individual birds, eliminating the risk of capturing multiple birds or non-target species. Our research suggests that trapping techniques are not necessarily universal across populations, and careful consideration of behavior and life history traits can improve targeted research for species like Northern Harriers.

Equipped with the trapping techniques developed in Chapter 1, we studied the habitat selection of breeding adult female Northern Harriers across multiple spatial scales in Suisun Marsh, California, in Chapter 2. We measured fine-scale microhabitat characteristics at nests, extracted macrohabitat characteristics across the landscape, and examined breeding home range habitat selection in adult female Northern Harriers captured at the nest and equipped with GPS/GSM transmitters. At the microhabitat scale we found that Northern Harriers select tall emergent and terrestrial vegetation, which is consistent with habitat selection studies in populations across their range. This result also suggests a selection for both marsh habitat and upland habitat for nest sites. Specific to Suisun Marsh, we found that Northern Harriers also have a high probability of selecting nest sites with California Rose (*Rosa californicus*). Macrohabitat selection consisted of nest placement ~ 100 m from water and revealed an avoidance of shrub vegetation. These results combined indicate a selection for vegetation structure and nest placement in vegetation that provides protection from mammalian predators. A subset of nests on the Grizzly Island Wildlife area avoided nest placement near all-terrain vehicle (ATV) tracks, and spatially clustered nests revealing additional adaptations for predator and disturbance avoidance as well as semicolonial nesting behavior. Small mammal densities had no effect on nest site selection, despite the known importance of small mammals, particularly voles, on Northern Harrier reproductive success. Lastly, we found that adult females had a significantly higher probability of wetland habitat use over any other habitat type even as home ranges expanded, and females foraged farther from nest sites across the nesting season. Our results inform habitat managers to maintain tall, undisturbed vegetation in both upland and marsh habitats while ensuring dry areas for nest sites are available with complex vegetation and habitat structure, like California Rose and nearby water, to provide protection from mammalian predators.

Chapter 3 builds on the research from Chapter 2 and examines the effects of multi-scale habitat characteristics on nest survival using logistic-exposure models. We found apparent nest success was relatively low (40%) compared to nest survival in populations across the Northern Harrier range, but Mayfield’s nest survival was similar to nests in Suisun Marsh three decades ago. Despite similar survival rates, the number of nests and nest density has declined over the past three decades, revealing a declining population with already low nest success. High spring small mammal densities had a positive effect on nest survival, and high summer small mammal density increased the number of fledglings. However, the California Vole (*Microtus californicus*) population is alarmingly low in Suisun Marsh compared to historical observations. Voles are an important prey species and improving their abundance could improve harrier nest survival and increase the breeding population in Suisun Marsh. Our results also show that a high proportion of live vegetation and the presence of residual vegetation at the nest are important microhabitat characteristics that influenced nest survival. Further, nests closer to California Rose also had higher nest survival, which is consistent with nest site selection determined in Chapter 2. Lastly, nest survival was highest in managed marsh habitat, despite potential selection for tidal marsh habitat. Lower nest survival in tidal marsh habitat may result from inappropriate habitat structure and extreme flooding events that could be exacerbated by sea level rise in the future. Restoring tidal marsh to large, contiguous habitat patches with numerous smaller channels to better diffuse the effects of high tides across the tidal plane could reduce nest flooding for harriers and other sensitive tidal marsh species in Suisun Marsh.

Chapter 4 focuses on migration ecology of Northern Harriers wintering in Suisun Marsh. Using the winter trapping techniques developed in Chapter 1, we marked adult females with GPS/GSM transmitters in this first study of Northern Harrier migration ecology and habitat selection across their annual cycle. We recorded a total of 18 spring and 11 fall complete (round-trip) and partial (one-way) migrations for 14 individual Northern Harriers and identified nest sites across five Western United States (AK, CA, ID, OR, WA). We also recorded the three longest-distance migrations for any Northern Harriers to date across two individuals breeding in Alaska, ranging from 13,000 to nearly 20,000 km traveled roundtrip. Of the 11 fall migrations recorded, all birds returned to Suisun Marsh, highlighting its importance in Northern Harrier wintering ecology in Western North America. Mean spring migration was shorter than mean fall migration by nearly two months, with fewer stopovers and a faster migration speed (~ 200 km d^{-}

^{1}) suggesting strong selection pressure to reach the breeding grounds early to secure a mate and territory, and to increase reproductive success. Migration timing is generally consistent with known timing for this species from raptor migration monitoring stations across North America. Migration routes were primarily along central and eastern corridors through California, Washington, and Oregon, and generally continued along inland intermountain regions through British Columbia and into Alaska for long-distance migrants. Wetland habitat was the most consistently selected habitat type across the annual cycle, with grassland and shrubland habitat also selected at stopover locations, and cultivated habitat also selected during the winter. Though habitat selection varied across the annual cycle, many breeding areas and stopover locations occurred on protected state and federal lands, which provide a unique opportunity for focused management and conservation efforts for migratory Northern Harriers. Raptor migration monitoring and banding stations located throughout Western North America may be misaligned with Northern Harrier migration, leading to low detections and population estimates because migration occurred along corridors where migration monitoring and banding stations are not located. Focusing migration monitoring along wetland habitat corridors and increasing breeding population research could improve Northern Harrier management and conservation efforts.

Chapter 1: To catch a (marsh) predator: Modified trapping methods for breeding and wintering Northern Harriers (*Circus hudsonius*)*

Shannon M. Skalos[1,2], Michael L. Casazza[2], Matthew J. Falcon[2], William Thein[2], Joshua M. Hull[1]

[1] University of California, Davis. One Shields Avenue, Davis, CA 95616, USA

[2] U.S. Geological Survey, Western Ecological Research Center, 800 Business Park Drive, Suite D, Dixon, CA 95620, USA

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Abstract

While there are a variety of methods available for trapping raptors, some species, such as Northern Harriers (*Circus hudsonius*), are not amenable to capture with standard methods. We tested several existing trapping methods and modified two of them based upon Northern Harrier ecology and behavior across seasons in our study population in California. No previously successful methods described in the literature were effective in our study population. Two modified methods emerged as the most effective for trapping Northern Harriers: 1) placing two dho-gazas around the nest in a V-shape and flushing the adult female into the nets during the breeding season, 2) using remote-triggered bow nets baited with waterbird carcasses to promote scavenging in winter. Dho-gazas at the nest work well during the early nesting stage when nestlings are less than two weeks old and adult females are most attentive. However, the youngest nestling must be old enough to thermoregulate during the trapping and post-trapping period to reduce risk of mortality. This method is not suitable during the incubation stage because Northern Harriers are prone to nest abandonment. In the winter, Northern Harriers are known scavengers, yet this aspect of their behavioral ecology has not previously been exploited and documented for trapping purposes. These two methods allow for selective Northern Harrier trapping across seasons and provide modified options for research on this understudied and declining species in North America.

1. Introduction

Northern Harriers (*Circus hudsonius*) are a common raptor species found across wetland and grassland habitats throughout North America (Smith et al. 2020). Though common, Northern Harriers are in decline across their range despite being listed as Least Concern (but decreasing) by the International Union for Conservation of Nature (BirdLife International 2016). In the United States, Northern Harriers have no federal listing status, but they are listed as either endangered, threatened, critically imperiled, imperiled, vulnerable, high conservation need, or as a species of special concern across 23 states. In Canada, Northern Harriers are considered “not at risk” though “declines in numbers have been noted in some areas” (COSEWIC 2019). Northern Harriers have no special listing status in Mexico or any Central American countries. As their populations decline, and wetland and grassland habitats continue to be lost across North America, it is imperative that we understand Northern Harrier ecology as top predators in these sensitive ecosystems (Sergio et al. 2006, 2008; Donázar et al. 2016).

Northern Harriers are an elusive species and are particularly secretive during the breeding season because their nests are located on the ground in tall, dense vegetation and because of their terrestrial perching and roosting behavior (Smith et al. 2020). Additionally, Northern Harriers regularly evade traditional raptor trapping methods, like bal-chatris (Simmons 2000). As such, Northern Harriers are an understudied species with few recent published studies. Older long term studies include well-known research in Wisconsin, USA (e.g., Hamerstrom 1963, 1968, 1979, 1986; Scharf and Hamerstrom 1975, Hamerstrom and Kopeny 1981, Hamerstrom et al. 1985), and in New Brunswick, Canada (e.g., Simmons and Smith 1985, Simmons et al. 1986b, a; Barnard et al. 1987, Simmons 1988). Given their elusive behavior, trapping Northern Harriers for targeted research studies can be difficult.

Methods used to capture Northern Harriers have included bal-chatris baited with live European Starlings (Sturnus vulgaris, Berger and Hamerstrom 1962), modified bal-chatris (called a "nest dome") placed over nestlings in the nest (Hamerstrom et al. 1985), bow nets over the nest (Hamerstrom 1963), and a dho-gaza at the nest with a live or taxidermy-mounted (hereafter, "mounted") Great Horned Owl (Bubo virginianus, hereafter, "owl"; Hamerstrom 1963). Surprisingly, bal-chatris with live bait worked well during the non-breeding season in Wisconsin resulting in nearly 100 Northern Harrier captures across several years, but were ineffective during the breeding season with only four captures (Hamerstrom 1963). The closely related Hen Harrier (*Circus cyaneus*) also does not respond to bal-chatris during the breeding season (Picozzi 1977), and Simmons (2000) stated "…harriers won't touch, and rarely see, a noose-covered Balchatri trap baited with mice or birds,…" Thus, alternative methods for trapping harriers are needed.

The success of bal-chatris with live lure birds can, in part, be attributed to the specific methodology used by Hamerstrom and colleagues. For example, traps were placed around an area (4–5 traps for up to 20 acres) with known raptor activity and left out mostly unsupervised for 6–24 hours (Berger and Hamerstrom 1962), a method known as line trapping (Bloom et al.

2007). Line trapping, much like noose carpets, can result in the ability of individuals to escape and incidental captures of non-target species (Bloom et al. 2007). However, modern line trapping is greatly aided by the use of trap monitors that signal when traps have been triggered, allowing researchers to retrieve trapped birds quickly (Bloom et al. 2007). Nonetheless, this method can be labor and time intensive, and requires care of live lure animals.

Dho-gazas at the nest with a live or mounted owl were the most effective method during the breeding season in Wisconsin, while a nest dome over nestlings worked well for adults not trappable using dho-gazas with an owl. The combination of these two methods resulted in captures of over 200 breeding Northern Harriers across a 24 year study period, the majority of which were adult females (Hamerstrom 1963, Hamerstrom et al. 1985). Western Marsh Harriers (*Circus aeruginosus*) and at least one Black Harrier (*Circus maurus*) have been captured successfully with a bal-chatri on the nest (presumably a "nest dome"), as well (Garcia-Heras et al. 2019, Vansteelant et al. 2020). Dho-gazas with various mounted owl species have also worked with Hen Harriers (Picozzi 1977), Black Harriers (Garcia-Heras et al. 2019) and Montagu's Harriers (Circus pygarus; Vansteelant et al. 2020), though trapping effort and success were not always reported. Pallid Harriers (*Circus macrousus*) have been captured with a similar technique, but using a mounted Corsac Fox (*Vulpes corsac*) instead of an owl (Terraube et al. 2012). However, dho-gazas and an owl at the nest have not worked as successfully in other Northern Harrier populations or in African Marsh Harriers (Circus ranivorus, e.g., Simmons et al. 1986a, Martin 1987, Simmons 2000) and are ineffective for capture during the non-breeding season (Hamerstrom 1963, Bloom et al. 1992). With such mixed success, more reliable methods that can be used across populations and seasons are needed.

To study breeding and wintering Northern Harriers across their annual cycle and maximize trapping success, we tested several existing methods, as well as developed modified trapping methods that are specific to Northern Harrier behavior and ecology. In this paper, we describe the trapping methods attempted and focus on discussing two modified methods that emerged as successful. It is our hope that these modified methods will facilitate more research on Northern Harriers that have potentially been overlooked due to their trapping difficulty and provide modified methods for trapping other harrier species.

2. Methods

2.1 Study Area

This study was conducted in Suisun Marsh (hereafter “Suisun”, pronounced “soo-soon”), which is a large (~ 46,950 ha) brackish water estuary in the San Francisco Bay Delta Watershed located in Solano County, California and is a native land of the Suisun tribe of the Patwin Native Americans. Within Suisun, we worked primarily on the Grizzly Island Wildlife Area (~ 5,250 ha), owned by the California Department of Fish & Wildlife, as well as adjacent private duck hunting clubs and properties owned by non-profit organizations. Habitat types in Suisun consist of tidal and diked managed marshes, herbaceous upland fields primarily managed for nesting waterfowl, and cattle and sheep pastures. The dominant vegetation across Suisun includes bulrushes (*Schoenoplectus* spp.), cattails (*Typha* spp.), rushes (*Juncus spp.*), pickleweed (*Salicornia virginica*), various forbs (e.g., *Atriplex patula, Lepidium latifolium*), grasses (e.g., *Distichlis spicata, Frankenia salina, Bromus* spp., *Elymus* spp., *Hordeum* spp.), shrubs (e.g., *Rosa californica, Baccharis pilularis*), and Eucalyptus trees (*Eucalyptus* spp.).

Suisun has the highest documented Northern Harrier nesting density in California, and Northern Harriers are abundant in wetland and grassland ecosystems, like Suisun, during migration and winter (Shuford and Gardali 2008).

2.2 Breeding Season Trapping Methods

Breeding season trapping methods were tested across three seasons (2017–2019). We used several methods for trapping Northern Harriers at the nest: 1) Dho-gazas or mist nets placed in a V-shape or parallel formation near the nest and baited with either a mounted (Fig. 1.1 A) or live owl (Fig. 1.1 B) in the center of or between the nets to facilitate active aggression by adults. 2) A modified bal-chatri ("nest dome") that fit over nestlings to entice adult females to land at the nest (Fig. 1.1 C). 3) A handheld dip net used to try to capture the adult female while brooding at the nest (Fig. 1.1 D–E). 4) Two dho-gazas placed in a V-shape directly around the nest coupled with handheld dip nets to flush adult females into the nets (Fig. 1.1 F). 5) Remote-triggered bow nets baited with various waterfowl species or American Coot (hereafter, "coot"; *Fulica americana*) carcasses (collectively hereafter, "waterbirds") to facilitate scavenging placed near the nest and camouflaged with grass (Fig. 1.2).

In 2017, we used one or two mist nets (60 mm mesh, 210/2 denier/ply, 4 shelves, 2.6 m height, Avinet Research Supplies, Portland, ME) as described above (method 1; Fig. 1.1 A). The mounted owl was equipped with an internal servomotor that could rotate the head 180 degrees with a remote control. We also placed a small speaker underneath the owl that played various owl calls on a loop during trapping events. When the breeding pair detects the owl, this elicits an aggressive response that consists of adult birds swooping down and attempting to attack the owl resulting in capture in the nets (Hamerstrom 1963, Bloom et al. 1992). Nets were placed on 3-m tall conduit poles (1/2 in x 10 ft Electric Metallic Tube (EMT) Conduit, Allied Tube & Conduit, Harvey, IL) camouflaged with spray paint that were either placed directly into the ground ~ 0.5 m deep, or fitted over a 1-m long rebar pole placed ~ 30 cm into the ground. Where vegetation at the nest was over 1 m tall, we extended the poles by placing them on top of 1–1.2 m tall sections of conduit connected with a coupler. The tops of nets were placed as close to the top of the poles as possible to maximize height of the nets. We used a mounted owl in 2017 because we did not have access to a live owl, and we used mist nets instead of dho-gazas to increase the length of the net for capture and prevent collapse in high winds. Additionally, we attempted capture at the nest by placing a nest dome over the nestlings in the nest (method 2, Fig. 1.1 C).

In 2018, we used a live owl positioned in the center of and directly below one dho-gaza (3.2 cm mesh, 1.83 m x 1.83 m) on the same metal poles described above placed just outside of the nest (method 1; Fig. 1.1 B). A dho-gaza was used instead of a mist net due to birds bouncing out of mist nets in 2017. The owl was positioned on a metal T-perch placed into the ground and tethered with leg jesses. We also attempted capture of adult females at the nest by placing a nest dome over the nestlings in the nest (method 2; Fig. 1.1 C). Additionally, we attempted to capture brooding females at the nest with a handheld dip net only (method 3; Figure 1.1 D –E; e.g., Ranger Big Game Landing Net, 48 in Handle, 34 in x 30 in Hoop, Ranger Nets, Detroit, MI), or in combination with two dho-gazas placed in a V-shape at the nest, with the nest in the center of the nets (method 4; Fig. 1.1 F). The opening of the nets was facing the wind direction as females always enter the nest by flying into the wind (pers. obs.). An observer watched the female return to the nest with binoculars from a distance, while another observer was hidden and camouflaged near the nest. We used two-way radios to communicate when the female had landed so the hidden observer could run in quickly and flush the female into the nets before she could escape.

This method was modified from its successful use in capturing nesting American Bitterns (*Botaurus lentiginosus*), which nest on the ground in wetland and grassland habitats and have similar nest characteristics to Northern Harriers (Huschle et al. 2002). Finally, we also used remote-triggered bow nets (method 5; 5 ft remote-triggered bow net, Mike's Falconry Supplies, Gresham, OR) baited with a waterbird carcass placed just outside of the nest (Fig. 1.2) to facilitate scavenging by adults, a method that was successful in the winter (see results).

In 2019, we used two dho-gazas in a V-shape placed at the nest and flushed females into the nets (method 4; Fig. 1.1 F). This was the primary method used due to its success in capturing adult females in 2018.

Figure 1.1. Breeding season trapping methods used at Northern Harrier nests: A) two mist nets with a mounted owl in the center; B) Dho-gaza with a live owl below the net; C) nestlings inside of a modified bal-chatri ("nest dome") at a nest (rabbit leg placed on top of the trap by the adult female); D) a researcher approaching a nest with a handheld dip net; E) two researchers approaching a nest from both sides with handheld dip nets; and F) an adult female Northern Harrier being flushed off of a nest into a dho-gaza (researcher with handheld dip net not pictured). Photo credit: William Thein and Shannon Skalos, USGS.

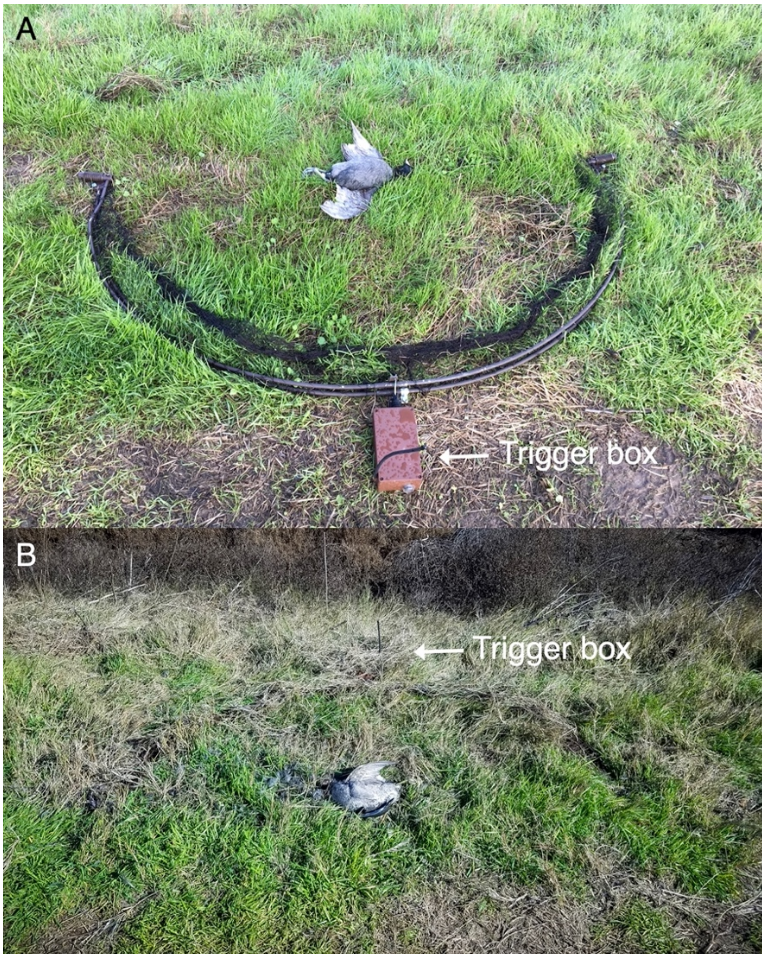

Figure 1.2. Remote-triggered bow net baited with an American Coot carcass (A) and camouflaged with grass (B). The trigger box with black antenna is indicated by the white arrow. Photo credit: William Thein and Shannon Skalos, USGS.

In both 2018 and 2019 trapping attempts at the nest were limited to when the youngest nestling was capable of thermoregulation (> 5 d of age), and before the youngest nestling was old enough that females did not return to the nest frequently to feed, brood, and nest build (< 14 d of age; see results). During these first two weeks of brooding, females were most attentive to nestlings and more frequently left and returned to the nest with nest material (Fig. 1.3) or prey, increasing our chances for capture. Additionally, the youngest nestling needed to be at least ~ 5 d of age because adult females could be off the nest for up to 2 hr during the trapping attempt, plus an additional 1–2 hr if captured and outfitted with a transmitter before they resumed normal nest attendance behavior.

Trapping attempts for all methods typically occurred between sunrise and noon either before females left the nest or during active foraging and nest attendance behaviors in the morning and while temperatures were relatively cool. Each trapping attempt lasted an average of 2 hr, but typically less depending on the method used. Because we only visited nests every 4–5 d to minimize disturbance, we were limited to only 2–3 trapping attempts per nest.

Figure 1.3. An adult female Northern Harrier approaching her nest carrying nest material in her mouth with two dho-gazas positioned around her nest in a "V" formation. Photo credit: William Thein, USGS.

2.3 Winter Season Trapping Methods

We trapped in Suisun on the Grizzly Island Wildlife Area in three locations where there were raised levees between managed marsh units suitable for placing and viewing traps from a distance. Winter trapping occurred over three seasons: January to February 2018, December 2018 to March 2019, and December 2019 to January 2020. These time periods were chosen to maximize capture of wintering migrant individuals.

We used two methods for winter trapping: 1) Noose carpets, and 2) remote-triggered bow nets baited with various waterbird carcasses and camouflaged with grass. Noose carpets and bow nets are commonly used methods for trapping wintering and migrating raptors, but typically use live lure animals instead of carcasses (Bloom et al. 2007). We consulted with an airport airstrike prevention biologist who documented successful trapping of Northern Harriers in Utah using noose carpets and self-triggered bow nets (Tordoff 1954) baited with waterbird carcasses (Mike Smith pers. comm.). Northern Harriers are known to scavenge on waterbirds in the winter (e.g., Blohm et al. 1980, Peterson et al. 2001, Soos and Wobeser 2006), and have even been incidentally captured in a trap using a waterfowl carcass (Godfrey and Fedynich 1988), yet this aspect of their behavioral ecology has rarely been systematically exploited for trapping to our knowledge. Northern Harriers have also been documented attacking and sometimes successfully killing live waterbirds in the winter (Hammond 1948, Collopy and Bildstein 1987). Indeed, in our own population we have observed individuals regularly scavenging or stooping on waterbirds and Ring-necked Pheasants (*Phasianus colchicus*). As such, we hypothesized that passive trapping with waterbird carcasses would be successful at our study site in the winter.

Because our study was targeting adult females for transmitter deployment, we decided to use remote-triggered bow nets instead of self-triggered bow nets for targeted selection of individuals at the traps and to reduce the amount of time individuals spent in traps after capture. However, we ultimately captured every Northern Harrier that landed at a trap because they would often return repeatedly if only flushed away, preventing other individuals from being trapped. We placed bow nets (Fig. 1.2) and noose carpets (Fig. 1.4) camouflaged with grass ~ 200 m apart on raised levees by staking them to the ground with garden stakes. Bow nets could be tested, observed, and triggered via spotting scopes from an adjacent levee ~ 250–600 m away; far enough that birds were not disturbed by our presence, but close enough that we could easily drive to the trap after capture within a few minutes. We did not use a blind and simply stood on a levee outside of our trucks with spotting scopes. Trapping locations were in open marsh habitat away from trees and power lines to minimize attracting non-target raptor species, like Red-tailed Hawks (*Buteo jamaicensis*).

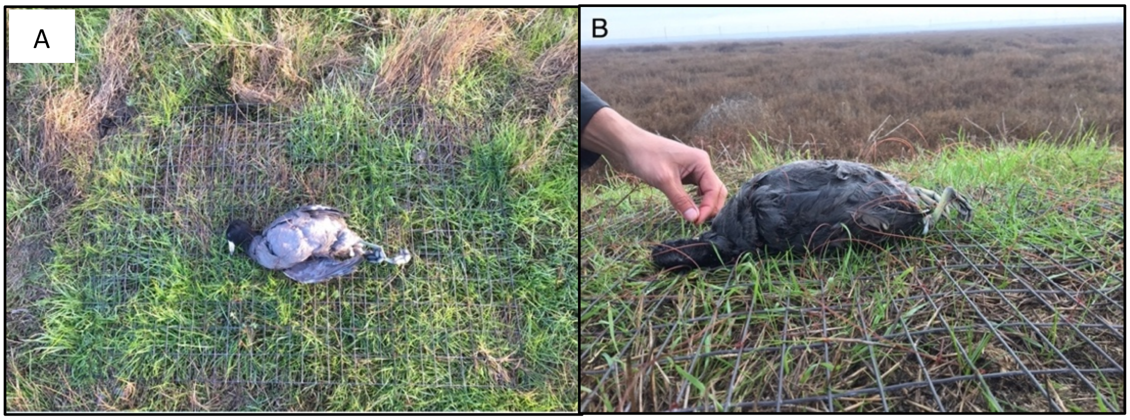

Figure 1.4 Top view (A) and side view (B) of a noose carpet baited with an American Coot carcass. Photo credit: Shannon Skalos, USGS.

In the 2017–2018 season, we used 1–7 noose carpets and one bow net per trapping day, before switching to three bow nets exclusively due to their superior trapping effectiveness. In the 2018–2019 season, we used 3–5 bow nets per trapping day with only one day of additional noose carpets because we were targeting a specific individual for transmitter removal. In 2019–2020 we used five bow nets per trapping day. We recorded the amount of time spent trapping; the number of individuals captured; the bait species on which individuals were captured; and the number, sex, and age of individuals that looked at traps but did not land or landed at or near traps but were not trapped.

All captured birds across seasons were identified to sex and age, measured for morphometrics (wing chord, tail length, tarsus depth, culmen length, hallux length, and weight), and banded with a USGS aluminum lock-on leg band prior to release. Some individuals were fitted with a transmitter using a Teflon backpack harness for a movement and habitat selection study.

3. Results

3.1 Breeding Season Trapping Results

The most successful trapping method was the use of two dho-gazas in a V-shape at the nest and flushing females into the nets (Table 1.1). This method resulted in the capture of adult females at 10 of 18 nests (56% capture success), across 22 trapping attempts for an average of 1.2 trapping attempts per nest. The average amount of time for each trapping attempt was 1.7 hr for a total of 38.3 hr. The average age of the youngest nestling (rounded to the nearest whole number) was 10 d, but 8 d for successful captures (Table 1.1). This method was most effective at nests with short vegetation that allowed nets to be erected above the vegetation and did not prevent nets from collapsing. Nests with very tall vegetation (> 2 m) were not suitable for this method.

The eight nests that were attempted with dho-gazas that did not result in a capture were either almost successful or were the result of uncooperative females that either never appeared during the trapping attempt or would not land at the nest with nets present (neophobic). Almost successful attempts were those where females were cooperative and returned to the nest but were able to depart the nest without hitting the nets, or hit and collapsed the nets but still escaped, or hit and did not collapse the nets and escaped. We knew a female was too neophobic to land at the nest if she repeatedly attempted to land but veered off as she approached while aggressively calling at the nets.

No other method tested resulted in any captures (Table 1.1). The only traditional method attempted frequently was the mounted or live owl with mist nets or dho-gazas at the nest, but this method also resulted in no captures (Table 1.1). We attempted a mounted owl seven times on five nests, for an average of 1 hr per trapping attempt and a total of 7 hr. The average age of the youngest nestling was 21 d old. Adult females were aggressive towards the owl, but almost never got close enough to be captured. Only two females ever hit the very top of a net and bounced out, after which they no longer would approach the owl or nets. Males almost never appeared during trapping attempts, and when they did, they only assisted females with nest defense for brief periods of time before leaving the females to continue nest defense alone. We used a live owl with a dho-gaza at three nests, for an average of 1.8 hr per trapping attempt and a total of 5.5 hr (Table 1.1). Despite the average age of the youngest nestling being only 6 d, individuals responded almost identically to how they responded to the mounted owl.

Table 1.1. Trapping statistics for all nest trapping methods, including number of nests attempted, total trapping attempts, number of captures, average age of youngest nestling (rounded to the nearest whole number), average trapping time per trapping attempt, and the total trapping time per method.

Trapping Method	No. Nest Attempts	Total Attempts	Total Captures	Avg. Age of Youngest Nestling	Avg. Trapping Time (hr)	Total Trapping Time (hr)
Mounted owl with mist net(s)	5	7	0	21	1.0	7
Live owl with dho-gaza	3	3	0	6	1.8	5.5
Bal-chatri over nestlings	3	3	0	12	1.1[d]	2.3
Bow net with waterfowl	2	2	0	17	1.3	4
Dip net only	6	10	0	11	0.3	1.3
Dho-gazas at nest with dip net	18	22	10 (56%)[b]	10 (8)[c]	1.7	38.3
Total/Average	27[a]	47	10	12	2.2	58.4

[a] The total number of nests attempted was 27, but multiple methods were attempted at the same nest for several nests, totaling to 37.

[b] Parentheses contain the percent of successful captures (number of nests captured/total number of nests attempted).

[c] Parentheses contain the average age of the youngest nestling rounded to the nearest whole number at successful captures.

[d] Only two nests included because at the third nest we used two methods at one trapping session and the time per method was not recorded.

3.2 Winter Season Trapping Results

In total, we captured 78 Northern Harriers across 40 total trap days and 205.5 total trapping hours using both noose carpets and remote-triggered bow nets across all three winter seasons (Table 1.2). Noose carpets resulted in five captures, one on a waterfowl carcass and four on coots. Bow nets resulted in 73 captures, 32 on waterfowl carcasses and 41 on coots. However, bow nets were our preferred trap and used more frequently than noose carpets. Across all trap types, we offered waterfowl and coots in approximately equal proportions (waterfowl = 55%, coots = 45%), and almost always offered both waterfowl and coots on each trap day in case individuals preferred one to another.

Of the 78 captures, eight were adult males, four were juvenile males, 55 were adult females, and 11 were juvenile females (Table 1.2). Adult females were by far the most common sex and age class present on the wildlife area, and also the most aggressive at defending traps or chasing away juveniles and adult males that landed at traps. As such, there were many individuals that looked at traps or landed at or near traps that were ultimately not captured. There were 17 adult males, 97 adult females, 25 juveniles, and 19 unknown individuals for a total of 158 Northern Harriers that flew over and looked at traps; and 12 adult males, 71 adult females, 11 juveniles, and 2 unknown individuals for a total of 96 Northern Harriers that landed at or near traps but were not captured (Table 1.3). In total, there were 254 incidents of individuals looking at or landing at or near traps but not captured (Table 1.3).

Table 1.2. Capture statistics for all winter trapping methods, including recaptures, across adult and juvenile males and females, total captures, total trap days, and total trapping time per trapping method and bait used.

Trapping Method	Adult Male[a]	Juvenile Male[b]	Adult Female[a]	Juvenile Female[b]	Total Captures	Total Trap Days[c]	Total Trapping Time (hr)
Noose Carpet	1	0	3	1	5	6 (0.83)	32.5
Waterfowl	0	0	1	0	1	-	-
American Coot	1	0	2	1	4	-	-
Bow net	7	4	52	10	73	38 (1.92)	201.0
Waterfowl	2	3	25	2	32	-	-
American Coot	5	1	27	8	41	-	-
Total	8	4	55	11	78	40 (1.95)[d]	205.5[e]

[a] Includes AHY and ASY individuals.
[b] Includes HY and SY individuals.
[c] Parentheses contain the number of captures per trap day.
[d] Total days is 40 d, but on some days both noose carpets and bow nets were used, totaling to 44 d when calculated separately.
[e] Total time is 205.5 hr, but on some days both noose carpets and bow nets were used, totaling to 233.5 hr when calculated separately.

Table 1.3. Trapping statistics for all winter trapping methods and bait types for adult and juvenile males and females that either flew over and looked at traps or landed at or near traps but were not captured. Numbers may include the same individuals counted several times.

Trapping Method	**Adult Male Looked**[a]	**Adult Male Landed**[a]	**Adult Female Looked**[a]	**Adult Female Landed**[a]	**Juvenile Looked**[b]	**Juvenile Landed**[b]	**Unknown Looked**[c]	**Unknown Landed**[c]	**Totals**
Noose Carpet	0	3	0	9	0	1	2	2	17
Waterfowl	0	0	0	0	0	0	1	0	1
American Coot	0	3	0	9	0	1	1	2	16
Bow net	17	9	97	62	25	10	17	0	237
Waterfowl	8	3	60	29	19	8	12	0	139
American Coot	9	6	37	33	6	2	5	0	98
Total	17	12	97	71	25	11	19	2	254

[a] Includes AHY and ASY individuals.

[b] Includes HY and SY individuals.

[c] Sex and age not recorded for these individuals.

4. Discussion

Two modified methods emerged as the most effective for capturing Northern Harriers in the breeding and winter seasons. The most successful method for capturing breeding individuals at our study site was two dho-gazas placed in a V-shape around the nest and females being flushed into the nets. The most successful method for winter trapping at our study site was remote-triggered bow nets baited with waterbird carcasses to elicit scavenging. Both methods resulted in far greater adult female captures than adult males or juveniles. However, both methods allow for targeted capture of Northern Harriers across seasons.

4.1 Breeding Season

For the two dho-gazas at the nest to be successful, two main components needed to be considered: direction of wind and age of youngest nestling. Females at our study site were observed predictably entering the nests by always flying into the wind for controlled landing. Knowing this female behavior allowed us to strategically place the opening of nets to maximize trapping success. If there was little wind, we observed females landing at the nest before placing nets to determine her preferred direction of entry (which often corresponded to the same direction she would enter when windy). Occasionally, winds shifted during trapping, which visibly made landing at the nest difficult or impossible for females if the opening of the nets were in the wrong position. This is a minor limitation of this method and one that can be overcome with careful observation.

Second, the age of the youngest nestling greatly influences a female’s rate of visitation to the nest. Females were far more attentive to nestlings when they were younger than two weeks of age due to the nestlings’ needs for increased brooding and provisioning. This behavior was also noted in other raptor species, as well (Bloom et al. 1992). However, the youngest nestling should be older than ~ 5 d of age to be able to thermoregulate. Trapping attempts before this age could potentially result in death of the youngest nestling(s) as a result of successful capture and subsequent transmitter attachment on adult females, which reduces female nest attendance for several hours (unpubl. data). It is difficult to attribute nestling deaths directly to trapping or transmitter attachment since the youngest nestling(s) often died in our nests each year, especially in large broods, regardless of whether we made a trapping attempt or not (unpubl. data). Nonetheless, we recommend researchers avoid trapping attempts earlier than this age to minimize potential negative effects to nestling survival.

Hamerstrom and colleagues make no mention of an appropriate time period in which to trap at nests, though the potential problems with raptor nest disturbance at different times during the nesting stage are well known (Fyfe and Oldendorff 1976), and one other study mentions females abandoning nests after trapping attempts (Simmons et al. 1986a), leading us to believe attempts were made during the incubation period or when nestlings were too young. In our study population, females never abandoned after at least one egg had hatched. However, females easily abandon if disturbed too frequently during the incubation period and have even abandoned after accessing a nest for the first time for < 1 min to check the status of the nest during incubation (unpubl. data). We believe this to be one of the most important components of making this method successful, and one that should be carefully considered when timing capture attempts.

One major drawback to trapping at the nest is the potential to disturb vegetation at the nest and to create a trail that exposes the nest to both mammalian and avian predators. Accessing ground nests inevitably leads to trails even after the first entry, though this has been shown to not lead predators into nests in other ground-nesting species (e.g., MaCivor et al. 1990, Skagen et al.

1999). We were still careful to use high steps in the vegetation to create footsteps rather than trails, and we always propped vegetation back up as we left the nest, if possible. Additionally, we would block the entrance to our trails with a thick wall of vegetation that we would gather from a nearby area. As a result, no females abandoned and no predators accessed or depredated nests due to our trapping attempts. Regardless of low nest predation in our population, we recommend limiting capture attempts at the same nest to minimize disturbance to nest vegetation, especially if the vegetation is composed of thin-stemmed grasses that are difficult to prop up after trampling, or if the nest will be regularly accessed for frequent nest visits.

Another drawback to trapping at the nest with our modified method is that it often limits captures to adult females. Rarely do males land at the nest, and because most females are usually not perturbed by the presence of the nets, they often do not alarm call or attract the attention of males to defend the nest. Other researchers have had limited success capturing males using noose-halos near mounted owls (Martin 1987) or dho-gazas and live owls at the nest (Bloom et al. 1992), and most notably Frances Hamerstrom captured numerous males (but significantly more females) at the nest using nets with an owl (Hamerstrom 1963). However, as previously discussed, this method has not worked well in other Northern Harrier populations or African Marsh Harriers (Simmons et al. 1986a, Martin 1987, Simmons 2000), nor was it successful in our study.

We acknowledge that in 2017 we likely attempted net captures with an owl too late in the nesting period when nestlings were too old and adults were less likely to defend the nest from predators (Bloom et al. 1992). However, when the same method was attempted in 2018 with a live owl and younger nestlings, we saw no difference in response from adults attacking the owl, with no birds coming close enough to hit the nets and adult males either not present or not participating for very long in nest defense. Further, our study site typically had clear, sunny skies and a light to strong breeze, which likely made the nets easily visible to adult birds at the nest. Indeed, Simmons (2000) pointed out that for this method to be successful, there must be overcast skies and no wind, which we imagine to be a major limitation to using this method in most populations (e.g., Martin 1987). This method does elicit a strong response, at least from the adult female, and has proven successful in other populations and species (Hamerstrom 1963, Picozzi 1977, Bloom et al. 1992, Garcia-Heras et al. 2019, Vansteelant et al. 2020). However, because it was the most time consuming and logistically difficult to setup, particularly when using a live owl, we do not believe it to be the most efficient method and we offer our modified method as an easier and more effective alternative to capturing breeding Northern Harriers and other harrier species, as well.

Regardless of which method we used, we limited our trapping attempts to 2 hr or less, when possible. Hamerstrom often trapped for several hours, sometimes up to 3 hr or longer, before capturing individuals at the nest (Hamerstrom 1963). We did not feel this was appropriate given how often nestlings needed to be fed, brooded, and, depending on the time of day, how high the ambient temperature reached. And as previously mentioned, females may take several hours to resume normal nest attendance behavior after capture and transmitter deployment. Thus, we wanted to minimize potential negative effects on nestling survival.

An important conservation implication for our modified breeding trapping method is potential increased protection of shorebird nests. Northern Harriers are considered nest predators for several sensitive shorebird species on the east and west coasts of the United States. Considerable effort is made for predator management at these breeding colonies, with the goal of capturing and relocating predators by exhausting all trapping methods before resorting to lethal removal. On the east coast where Northern Harriers have more legal protections, management can be challenging at shorebird colonies. Though dho-gazas with an owl have been reported to work on Northern Harriers at shorebird colonies in Southern California (Pete Bloom, pers. comm.), and have been scored as an effective method by expert opinion (Marcot and Elbert 2015), there is no documentation of the frequency of use or success rate of this method in the literature. Further, Manley (2016) found that Northern Harriers at Naval Base Coronado in San Diego, CA were not amenable to capture with baited bal-chatris, even though > 90% of raptors were captured with bal-chatris, and in two instances Northern Harriers were lethally removed after failed trapping attempts. There is no mention of using dho-gazas in this study despite spanning three breeding seasons. Lastly, a best practices guideline for predator management in Atlantic Flyway shorebird colonies lists “nest/egg destruction” and “anti-perching” as preferred methods to deter Northern Harrier predation (Hunt et al. 2019). In order to find a balance between shorebird and Northern Harrier management, it is clear that more effective trapping methods are needed to reduce lethal removal. We believe our modified method may help increase capture rates of breeding Northern Harriers for predator management at shorebird colonies.

4.2 Winter Season

Trapping Northern Harriers with remote-triggered bow nets baited with waterbird carcasses in the winter was very successful. Of a total of 40 trapping days and 205.5 trapping hours across three winter seasons, on only seven days did we not capture Northern Harriers, but we always attracted their attention or even had individuals land at traps but not be captured. Indeed, one of the seven days we were unsuccessful was one of the most active trapping days with several Northern Harriers at traps at once, all aggressively defending the traps but not settling, resulting in no captures.

Though Hamerstrom had success using bal-chatris with live starlings (Berger and Hamerstrom 1962, Hamerstrom 1963, Hamerstrom et al. 1985), we did not attempt this method largely due to it not working in other Northern Harrier populations or harrier species (Picozzi 1977, Simmons 2000), as well as the logistical challenges of acquiring and maintaining live lure birds and securing the necessary permits and IACUC protocols to do so. Other methods have been reportedly successful in other Northern Harrier populations and African and Western Marsh Harriers during the breeding season and may have success in the winter, like sprung-noose traps with live prey (Simmons 2000), noose-halo near a mounted owl (Martin 1987), or pole noose traps (e.g., Dunk 1991, Vansteelant et al. 2020). However, these methods had limited success or were tested on small sample sizes, so we did not test these methods in our population in either the breeding or winter season.

Using hunter-harvested and donated waterbird carcasses is relatively easy in a system where waterbird hunting is common. We recognize that acquiring waterbird carcasses may be difficult for some researchers in other study systems. However, it may be possible to use domestic waterbird and poultry carcasses obtained from commercial operations instead, though the efficacy of using different bait species should be tested since different harrier species may not be as attracted to prey species not common in their winter range. In a study on the closely related Hen Harrier (*Circus cyaneus*), individuals were attracted to and consumed dead rats and poultry chicks that were offered as supplementary food during the breeding season (Redpath et al. 2001), making these plausible alternative bait species.

Exploiting the scavenging behavior of wintering Northern Harriers using bow nets is a novel trapping method that has proven safe, effective, and easy (with previous unpublished success in Utah, Mike Smith, pers. comm., and with fish carcasses on three harrier species in India, Pete Bloom, pers. comm.). We believe this method can be applied across Northern Harrier populations, as well as other harrier species, for targeted trapping in the winter when harriers are more difficult to capture.

Combined with other methods, like bal-chatris and noose carpets, and depending on project goals, Northern Harrier captures could be well into the hundreds each winter trapping season. Like any trapping, we caution researchers to use their best judgment when it comes to balancing safety versus efficacy of trapping methods. For us, using remote-triggered bow nets rather than self-triggered bow nets and noose carpets was more conservative and likely resulted in fewer captures, but we felt it was the safest method for birds in our study population and aligned well with our study goals. Using trap monitors that alert researchers of captures could allow for increased trapping effort without the need for constant trap supervision (Bloom et al. 2007), potentially increasing capture rates.

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Chapter 2: Northern Harrier (*Circus hudsonius*) microhabitat and macrohabitat nest site selection in Suisun Marsh, California

Abstract

Understanding habitat selection is crucial to successful management and conservation of sensitive and listed species. How organisms interact with their environments is based on multiple spatial and temporal scales, which can have varying effects on reproduction and survival. In birds nest site selection involves assessing habitat at the microhabitat scale (e.g., vegetation structure at the nest), as well as at the macrohabitat scale (e.g., distance to suitable foraging habitat), which requires adequate protection of both habitats to maximize reproductive success. We studied the nest site habitat selection of Northern Harriers (hereafter "harriers", *Circus hudsonius*) at both micro- and macrohabitat scales in Suisun Marsh, California. At the microhabitat scale, harriers selected tall (~ 80 cm) vegetation in either marsh habitat with emergent graminoids or upland habitat with terrestrial graminoids, suggesting a selection for different habitat types, but similar vegetation structure. California Rose (*Rosa californicus*) was an important vegetation species, with nest sites most likely to contain 30-55% rose suggesting a selection for vegetation that provide protection from mammalian predators. At the macrohabitat scale, harrier nests across Suisun had a higher probability of nest sites at a specific distance from water (110-140 m) and far from unsuitable vegetation, like shrub species. Nesting near water, but not too close, represents a tradeoff between mammalian predator defense and nest flooding. Nesting far from shrubs also likely represents a predator avoidance strategy because mammalian predators use shrub habitat for refugia and are more likely to encounter nests in this habitat. Nests that occurred on the Grizzly Island Wildlife Area (GIWA) only differed in macrohabitat selection in that they were farther from all-terrain vehicle (ATV) tracks, suggesting an avoidance of human disturbance and/or mammalian predators that use ATV tracks as movement corridors through habitat. Nests were also more likely to be close to other harrier nests highlighting the semicolonial nesting behavior of harriers observed in other populations. Nesting near rose and away from shrubs was also an important selection criterion for nests on GIWA. Despite the known importance of small mammals, particularly voles, in harrier reproductive success, small mammal density did not affect nest site selection in our population. Lastly, we calculated the probability of habitat use within nesting adult female home ranges using GPS/GSM transmitters and found a significantly higher probability of wetland habitat use over any other habitat type even as home ranges expanded, and females foraged farther from nest sites across the nesting season. Our results inform habitat managers to maintain tall, undisturbed vegetation in both upland and marsh habitats while ensuring dry areas for nest sites are available with complex vegetation species and habitat structure, like California Rose and water on the landscape to provide protection from mammalian predators.

1. Introduction

Habitat selection is a key component to developing management and conservation strategies for sensitive species. Understanding habitat selection can inform conservation and management practices at different spatial scales (McGarigal et al. 2016). For example, mobile bird species may select a specific habitat type for their nest site but may also require suitable nearby foraging habitat that is different from nest site habitat within the breeding season (Steele 1993, Sergio et al. 2003, Barbaro et al. 2008). Thus, nest site selection involves assessing habitat at the microhabitat scale (e.g., vegetation structure at the nest), as well as at the macrohabitat scale (e.g., distance to suitable foraging habitat), which requires adequate protection of both habitats. These selection decisions represent a complex tradeoff between maximizing nest concealment and foraging efficiency and minimizing predation risk, among other things, which ultimately maximizes survival and reproductive success (Forstmeier and Weiss 2004, Miller et al. 2007, Dyson et al. 2019).

Even after multi-scale selection is determined, management goals and required management strategies can vary across spatial scales, from improving species-specific fine-scale habitat quality (i.e., the goal of most habitat selection studies), to large-scale habitat restoration (Razgour et al. 2011, Zhang et al. 2018). For example, Blakey et al. (2019) found that California Spotted Owls (*Strix occidentalis occidentalis*) select different canopy cover and tree sizes within old-growth forests across spatio-temporal scales, and that owls make foraging forays outside of Protected Activity Centers (PACs) during the breeding season, suggesting PACs designed to protect nest sites are too small. Likewise, Timm et al. (2016) used a multi-scale modeling approach and found that Mexican Spotted Owl (*S. o. lucida*) selection for high canopy cover within their PACs has resulted in mismatched management practices. Practices like reduced forest thinning not only increase smaller diameter trees unsuitable for nesting or roosting, but also increases wildfire risk within these protected areas. Results from studies like these fill important knowledge gaps about behavioral and ecological processes across spatio-temporal scales that improve habitat protection and connectivity across the landscape.

Multi-scale habitat selection research is being facilitated by the continued improvement of animal telemetry technology (Bridge et al. 2011, Kays et al. 2015). Transmitters have been reduced in size while simultaneously increasing the quantity and resolution of location data (e.g., GPS transmitters). This allows for better understanding of movement, space use, and habitat selection of animals across trophic levels, ultimately leading to improved understanding of ecosystem functioning (Kays et al. 2015) and more targeted conservation and management practices (Bonnot et al. 2009, Lockyer et al. 2015, Jedlikowski et al. 2016) by incorporating fine-scale habitat characteristics measured on the ground (e.g., nest site habitat characteristics) with larger-scale habitat use across the landscape from transmitter data (e.g., home range and foraging areas).

Among birds, raptors have provided some of the most fine-scale telemetry data, but studies have been limited to mostly large species, like eagles (e.g., Krone et al. 2009, Millsap et al. 2014, Watson et al. 2014, Balotari-Chiebao et al. 2016, Singh et al. 2016, Murphy et al. 2017, Murgatroyd et al. 2018, Ramos et al. 2019), vultures (e.g., Houston et al. 2011, Holland et al. 2017, Zvidzai et al. 2020), and large *Buteos* (e.g., Fleishman et al. 2016, Vansteelant et al. 2017), falcons (e.g., Prommer et al. 2012, Dixon et al. 2017, Hadjikyriakou et al. 2020), and kites (e.g., Panuccio et al. 2014, Pfeiffer and Meyburg 2015), while smaller species have mostly been excluded. Regardless of size, raptors are considered indicators of ecosystem health that bolster or are associated with ecosystem biodiversity through resource facilitation, top-down control of prey species, and other factors linked to habitat selection (Sergio et al. 2006, 2008; Donázar et al. 2016). Raptors are also charismatic birds that often serve as flagship species for research and conservation efforts (Sergio et al. 2006, 2008; Donázar et al. 2016). As such, raptors have received extensive research attention regarding their foraging ecology, reproduction, and migration. However, most studies focus on diurnal, tree-nesting or cavity-nesting species (e.g., Baker-Gabb 1983, Kübler et al. 2005, Wendt and Johnson 2017); species adapted to nesting in urban areas (e.g., Sodhi et al. 1992, Boal and Mannan 1999); and migration timing, abundance, and distribution of species across migratory corridors via hawk watches, banding stations, and band recoveries (e.g., Hull et al. 2012, Jaffré et al. 2013, Millsap et al. 2014). Elusive nocturnal and ground-nesting species (often nesting in wetland and grassland ecosystems) are more difficult to study and have received less research attention (e.g., Booms et al. 2014, Ibarra et al. 2014, Donázar et al. 2016, Keyes et al. 2016).

Compared to forests, wetland and grassland ecosystems have fewer native raptor species that serve as indicator species, yet candidate species do exist (Knopf 1994, Browder et al. 2002, Wright and Wimberly 2013, Zmihorski et al. 2016, Niemuth et al. 2017). Wetlands and grasslands are also two of the most threatened habitats in North America, and as such, many bird species specializing in these habitats have experienced significant declines. Wetlands have been reduced by > 50% since the late 1700's in the lower 48 United States (Dahl 1990), and California has lost more wetland habitat than any other state with > 90% lost (Dahl 1990, Garone 2007) with associated grassland habitats suffering similar losses (Garone 2007). Though total wetland loss has slowed in recent decades, largely from increased waterfowl management through the North American Waterfowl Management Plan (Dahl 2009, NAWMP 2018), salt marshes are still experiencing significant reductions (Dahl 2009). Overall, wetland and grassland habitat loss across North America has contributed to > 50% decline in wetland and grassland bird species, respectively (NABCI 2019, Rosenberg et al. 2019). Determining appropriate indicator species for wetland and grassland ecosystems may have important implications for habitat and species conservation and management plans.

Northern Harriers (*Circus hudsonius*; hereafter "harriers") are a relatively small (< 600 g) grassland and wetland specialist raptor species found across North America (Smith et al. 2020). Though harriers are widely distributed, they face significant declines in the Northeast and Midwest, where wetland and grassland habitats have experienced severe losses. It is in these regions where harriers have also received the most research attention (e.g., Hamerstrom 1969, Hamerstrom et al. 1985, Simmons and Smith 1985, Simmons et al. 1986b). In the West, however, harriers are largely unstudied despite declining population trends (Slater and Rock 2005, Shuford and Gardali 2008). In California, harriers are considered a Species of Special Concern, which highlights the need for more research into their threats, biology, and ecology to prevent further declines and being placed on the state endangered species list (Shuford and Gardali 2008).

Our goal was to examine harrier habitat selection across three spatial scales (microhabitat, macrohabitat, and home range) in Suisun Marsh, CA (hereafter "Suisun", pronounced "soo-soon"), the largest remaining contiguous brackish water marsh on the North American west coast. Incidental nest discoveries during waterfowl research show that Suisun has one of the highest historically documented harrier nesting densities in California(Loughman and McLandress 1994). Despite their known nesting abundance, there have been no targeted studies on harriers in Suisun to date. We predicted that harrier microhabitat nest site selection would be similar to studies in other parts of their range, where harriers generally select tall, dense vegetation at the nest (Hamerstrom and Kopeny 1981, Toland 1985, Dechant et al. 1998, Evrard and Bacon 1998). At the macrohabitat scale we predicted harriers would maximize distance to sources of human disturbance, like roads and structures (Dechant et al. 1998, Herkert et al. 1999), as well as potential predators, like stick-nesting raptors and trees (Herkert et al. 1999), but minimize distance to other harrier nests since they have been described as semicolonial nesters (Hamerstrom 1969, Simmons and Smith 1985). At the micro and macrohabitat scale, we also investigated harrier selection for specific vegetation species that could result in management conflicts, like invasive Common Reed (*Phragmites australis*). Lastly, we predicted harrier home ranges would reveal important foraging habitat that potentially differs from nest site habitat based on observations of foraging habitats and distances from nests described in other studies (Martin 1987). As central-place foragers during the breeding season, we predicted small mammal abundance within varying home range sizes would influence nest site selection.

2. Methods

2.1 Study Area

This study was conducted in Suisun Marsh, CA on the Grizzly Island Wildlife Area (GIWA) and surrounding private duck hunting clubs and properties owned by non-profit organizations (38.1515° N, 121.9717° W, Fig. 2.1, see detailed description in Chapter 1).

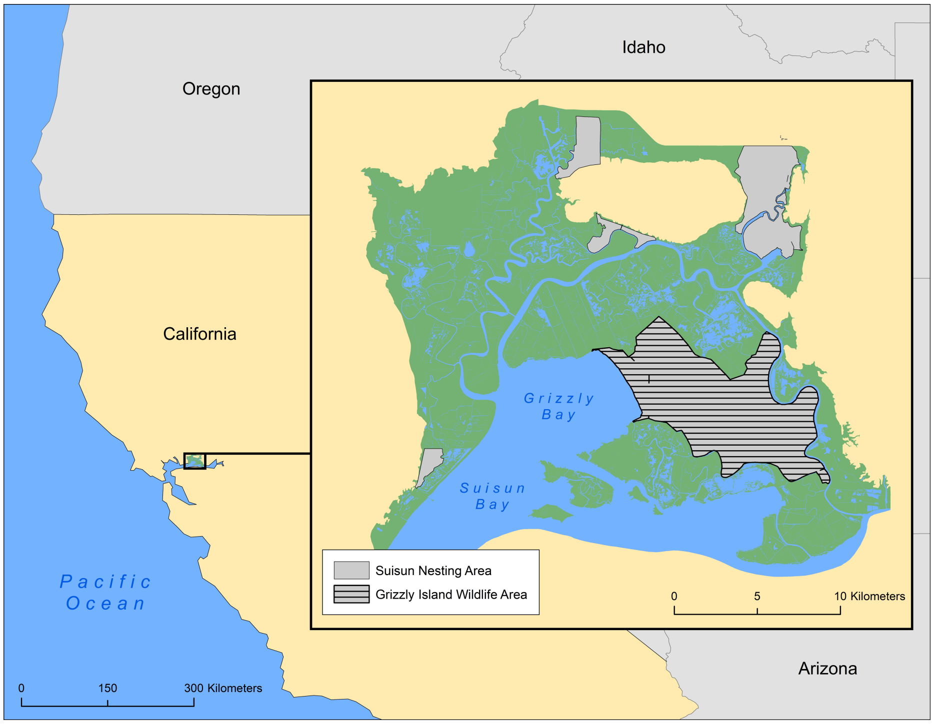

Figure 2.1. Map of Suisun Marsh (inset) located within the San Francisco Bay Estuary (black box) along the California coast. Nesting areas (gray) only represent locations where nests were

found, not the total area searched. The main Grizzly Island Wildlife Area is represented by hashed black lines. Data sources: states_basic layer, owner: cfitzpatrick, retrieved from: https://www.arcgis.com/home/item.html?id=f7f805eb65eb4ab787a0a3e1116ca7e5 on 18 February 2020; Suisun Marsh 2015 Vegetation layer [ds2676], owner: California Department of Fish and Wildlife, retrieved from: https://www.arcgis.com/home/item.html?id=ff4cda5db35f44cb81caf0f6921dfbfc on 18 February 2020.

2.2 Nest Surveys and Access

We searched for harrier nests across three breeding seasons during April of each year (2017–2019). We searched approximately 43 km^2 for 148 hours in 2017, approximately 62 km^2 for 115 hours in 2018, and approximately 73 km^2 for 170 hours in 2019. Nest searching consisted of point surveys at pre-determined randomized locations spaced ≥ 1 km apart and in locations where habitat was suitable for nesting (i.e., we did not search the many duck hunting clubs that retained water on managed marshes into the spring season). Locations were moved slightly if necessary, depending on visibility in a 360-degree circle. Initial presence/absence of harrier nests was determined in a standardized 1-hour survey. If harrier activity was detected, then further surveys were conducted for ≥ 4 hours to pinpoint exact locations of nests. Surveys took place between ~ 7:00 and 13:00 hrs, after which harrier activity decreased. Surveys consisted of 1–2 researchers standing in the bed of or on the roof of a truck using a spotting scope and binoculars and scanning the horizon in a 360-degree circle. If harriers were detected, individuals were watched for possible nesting or pair bonding behavior (i.e., courtship displays, food exchanges, and nest building). Notes on the number of individuals, sex, age, behavior, and number of potential nests, as well as a bearing and approximate distance to each nest from survey locations were recorded at each survey. Incidental surveys continued into May and June if new nesting activity was detected while accessing previously identified nests.

Waterfowl researchers on the wildlife area also performed nest searches during a concurrent study by driving all-terrain vehicles (ATV) along tracks in upland fields with a rope connected between two ATVs. This method causes incubating females to flush from the nest, allowing researchers to determine nest locations. This method does not damage nests or eggs because the rope is elevated slightly above the ground. Waterfowl researchers using this method each year discovered a subset of harrier nests used in this study. Once harrier nests were found, they were reported to us for continued monitoring.

We began nest visits in early to mid-May once most nests began to hatch and to avoid disturbance during the incubation period to reduce risk of nest abandonment. Nests were visited every 4–5 days once eggs hatched to monitor status and record nestling growth.

2.3 Capture and Transmitter Deployment

Capture techniques for breeding harriers used in this study have been described in detail in Chapter 1 of this dissertation. As a summary, breeding individuals were captured across two breeding seasons (2018 and 2019) using two collapsible dho-gazas around the nest coupled with handheld dip nets to flush adult females into the nets. We targeted adult females for this study as they are most abundant across our study site and seasons, are easiest to capture, and were large enough for transmitters used in this study (transmitters with harnesses weighed less than or equal to ~ 3% body weight). All captured birds across seasons were measured for morphometrics (wing chord, tail length, tarsus depth, culmen length, hallux length, and weight) and banded with a USGS aluminum lock-on leg band.

We used Crex GPS-GSM transmitters (14 g, Ecotone, Poland) in 2018 and OrniTrack-10 GPS-GSM transmitters (10 g, Ornitela, Lithuania, Fig. 2.2 A) in 2019. Transmitters were primarily attached using a backpack-mounted harness made of Teflon (1/4 inch natural tubular Teflon tape, Bally Ribbon Mills, Bally, PA). The Teflon crosses at the breast in a "X" formation and sits at the top of the keel bone. The Teflon "X" is weaved through a small ≤ 2.5 cm patch of leather (light weight kangaroo leather, Mike's Falconry, Gresham, OR) cut into a hexagon with four slits for the Teflon to pass through. The Teflon is then sewn in the center to the leather patch to secure the cross point and prevent sliding of the harness over the keel blocking the crop (Figure 2.2 B; Christopher Briggs, personal communication; e.g., Steenhof et al. 2006). Transmitters were also glued to a thin (4.5 mm or less) neoprene pad, and pads were trimmed around the transmitter to provide a cushioned base against the birds' back. Teflon was sewn and secured with superglue at the attachment points on the transmitter. Nape feathers were trimmed with scissors to reduce feather coverage of the solar panels as necessary prior to release. Transmitters were programmed to take 0.5-2 hr interval location fixes in the breeding season, depending on battery performance and transmitter type. Ecotone transmitters performed less well than Ornitela transmitters resulting in less frequent fixes.

Figure 2.2. Ornitela transmitter on an adult female Northern Harrier (A), and Teflon cross-breast "X" harness design with leather patch to stabilize harness at the top of the keel (B). Photo credit: Shannon Skalos.

2.4 Small Mammal Trapping and Density Estimates

We sampled small mammals during the spring (March to early April) across three years (2017–2019) to estimate abundance prior to the harrier breeding season. Spring sampling allowed us to investigate how small mammal populations may affect nest initiation and nest site selection in the beginning of the breeding season. Because harriers nest and forage in all four major habitat types in Suisun (managed marsh, tidal marsh, upland fields, and pasture), we sampled all habitat types for small mammal abundance.

We sampled four 7 x 7 trapping grids (10 m spacing) with Sherman live traps (LFA Folding Live Capture Rodent/Rat/Mouse Trap, 7.62 x 8.89 x 22.86 cm; H.B. Sherman Traps Inc., Tallahassee, FL) in each habitat type (managed marsh, upland fields, and pasture) for a total of 12 grids. Additionally, we used trapping data from the California Department of Fish & Wildlife's (CDFW) long-term Salt Marsh Harvest Mouse (*Reithrodontomys raviventris*) monitoring at historic tidal and managed marsh locations during the same or similar trapping periods at four 6 x 10 grids (10–15 m spacing; two in tidal marsh and two in managed marsh). Thus, we had four grids each in upland fields and pasture, six grids in managed marsh, and two grids in tidal marsh for a total of 16 grids. However, in the 2017 spring trapping period only four grids were sampled (two tidal and two managed marsh) due to excessive winter rains and flooding causing most of our sampling grids to be inaccessible for trapping.

Grid sizes were different in dimension and number of traps because our permit only allowed for a maximum of 100 traps checked by a single permittee (of which SMS was the only permitted individual), while the CDFW trapping grids were larger as their team had several permitted individuals checking traps on any given trap day. Grids were randomly located within each habitat type, and two paired grids were sampled simultaneously (for a total of 98 traps per trap day checked for the 7 x 7 grids and 120 traps per trap day checked for the 6 x 10 grids). Traps were baited with millet seed and crushed walnut (2017) or a birdseed mix, including millet and crushed walnut (2018–2019; Ackerman 2002; Smith et al. 2014). Each trap had a small handful of cotton batting placed at the back of the trap for warmth and a large paper clip at the entrance to prevent trap doors from closing completely on harvest mouse tails (Smith et al. 2014). The gap created by the paper clip is not large enough to facilitate escape from the traps. In the spring trapping period, we also placed traps inside thermal insulator sleeves made from home insulation material (Reflectix 60.96 x 254 cm. Double Reflective Insulation Roll with Staple Tab Edge, 0.79 cm thickness, The Home Depot, Atlanta, GA).

After each grid pair was sampled, traps were removed and cleaned with a 10% bleach solution, and batting was discarded. Traps were reset 1–4 days later at two new trapping locations until all locations were sampled. Trapping locations were randomly assigned (by pair) each year. Grids were paired spatially to facilitate trap checking to meet permit requirements that the first trap of each grid be checked by no later than one hour after dawn. Traps were checked each morning and immediately closed, then opened in the evening just prior to sunset for three consecutive trap nights.

Each small mammal captured was identified to species, except rats, which were identified to genus (*Rattus* spp.). Each animal was marked with a Monel ear tag (Laser-etched, model #1005-1lZ, National Band & Tag Company, International Identification Inc., Newport, KY) stamped with a unique number for individual identification. The federally endangered Salt Marsh Harvest Mice (SMHM; *R. raviventris*) and Western Harvest Mice (*R. megalotis*) were identified to species in the field using a combination of measurements, including tail length, body length, tail to body length ratio, and tail diameter. These measurements were later analyzed in a multiple linear regression equation developed to differentiate between these two species for final species identification (Sustaita et al. 2011). However, because there are discrepancies between field and regression identification results, and these methods are still being refined, we combined both species and report them as only harvest mice (*Reithrodontomys* spp.) here. It should be noted, though, that 89% of harvest mice captured were identified as SMHM in the field, and the regression analysis identified 89% of harvest mice as SMHM.

We estimated small mammal density at a 250-m grid cell resolution and averaged estimates across 1 km^2 and 5 km^2 circles around each nest and random site to represent breeding core-use areas and 95% home ranges (see results below). Density was estimated using open spatial capture recapture models ("oSCR" package) using a normalized difference vegetation index (NDVI) raster as the predictor variable. NDVI has shown to be an effective predictor for small mammal abundance (Smith et al. 2017). We then converted density to abundance by multiplying density estimates by the number of rows in the state space (the extent of Suisun Marsh) used for the density estimation. NDVI was calculated from April multispectral satellite imagery (RapidEye and PlanetScope) from the Planet Open California Data Portal (Planet Team 2017) for each year (2017–2019) using the Image Analysis tool in ArcMap 10.7.1 and clipped to the extent of Suisun Marsh (the state space). All analyses were performed in Program R (version 3.6.3; R Core Team 2020).

We estimated density and abundance for each small mammal species captured, as well as all small mammals combined. We combined all species because voles (*Microtus* spp.) are considered the most important small mammal to harrier reproduction in other populations (Hamerstrom 1979, Hamerstrom et al. 1985, Simmons et al. 1986b), but we captured none to very few voles each year, and as such we were not able to calculate density and abundance for voles alone. We decided to use all small mammal species combined as a proxy for voles since the population trend of individuals captured for all species followed the same pattern across years (Fig. 2.3).

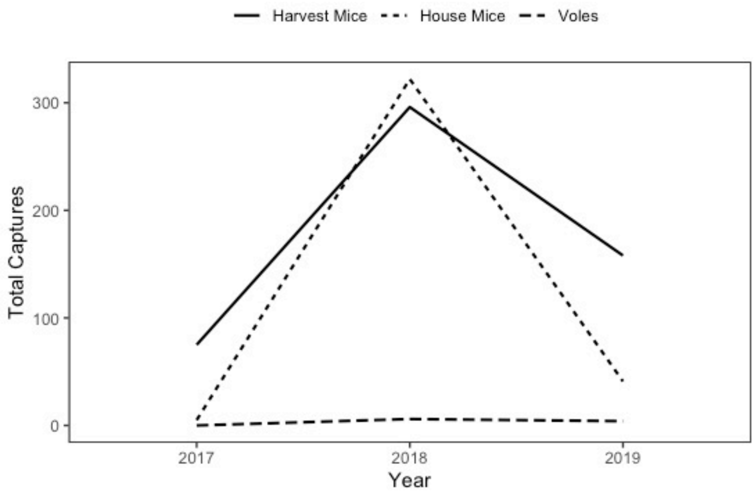

Figure 2.3. Total captures for Harvest Mice (includes both Western (*Reithrodontomys megalotis*) and Salt Marsh Harvest Mice (*Reithrodontomys raviventris*)), House Mice (*Mus musculus*), and California Voles (*Microtus californicus*) across three spring trapping seasons (2017–2019) in Suisun Marsh, CA.

2.5 Microhabitat Nest Site Selection

We measured nest and random site microhabitat characteristics at each nest after final nest fate was determined, which was at the current visit if the nest had failed, or 1–2 weeks after fledging if the nest was successful. We did not record habitat characteristics at the initial nest visit due to the prolonged disturbance time during measurements and the potential to cause nest abandonment, as well as the potential to trample vegetation at the nest. While measuring nest vegetation at nest initiation is the best method this isn't always logistically feasible because nests are often found well after initiation (McConnell et al. 2017). Harriers are also sensitive to nest disturbance during nest initiation and incubation (Hamerstrom 1969), and it isn't until after eggs hatch that the risk of abandonment decreases (Datta 2016).

At each nest, we recorded all vegetation species present, the percent composition by species, and the percent cover of live, dead, and residual vegetation within a 1-m radius of the nest bowl. Species were then categorized into functional groups relevant to life history traits in Suisun as emergent (wetland) graminoids (e.g., bulrushes, rushes, cattail), terrestrial graminoids (e.g., grasses), forbs (e.g., herbaceous plants), or shrubs (e.g., bushes, shrubs, trees, hard-stemmed woody plants) and summarized by percent present at each nest (Blondel 2003, Dyson et al. 2019). The height of the tallest species present, as well as the mean height of live, dead, and residual vegetation was also recorded using a Robel pole (Robel et al. 1970). The Robel pole was also used to measure the lateral cover (visual obstruction) of the shortest height of the vegetation around the nest at all four cardinal directions. A 1-m tall pole with an eye ring at the top is attached to the top of the Robel pole with a pre-measured rope spaced 4 m away at each cardinal direction. The shortest height visible on the Robel pole through the eye ring of the 1 m tall pole is recorded. We then averaged these measurements across all four cardinal directions to calculate an average visual obstruction height around each nest. Some nests had vegetation that was too tall to measure with our robel poles. We used the maximum height of the robel pole for these nests so as not to result in biased shorter averages had they been excluded. Lastly, we recorded the height and width of the nest bowl, as well as the length of any tunnels created by the nestlings leading away from the nest bowl. The same measurements were repeated at a paired random location generated with a random azimuth and distance within 5–50 m from the nest. These measurements and use of the Robel pole are consistent with methods used for waterfowl nest habitat measurements and other ground-nesting grassland birds (e.g., Ackerman 2002, Fisher and Davis 2010, Dyson et al. 2019). Each nest and random site were also assigned to one of three general habitat types: managed marsh, tidal marsh, or upland field (no nests were found in pasture in this study).

We then used conditional logistic regression to compare nest sites to paired random sites as the response variable (coded as binomial, 1 = nests and 0 = random sites), and the variables described above as predictor variables in a two-stage modeling approach. We used the glmer function from package "lme4" (Bates et al. 2015) with each nest and its paired site assigned to the same stratum (specified as a random effect) with a binomial family. All predictors were standardized to a mean of 0 and standard deviation of 1 prior to analysis. We assessed all pairwise predictors for multicollinearity by calculating Pearson's r coefficient and assessed the global model with variance inflation factor (VIF). Any predictors with a Pearson's r coefficient of $> |0.65|$ or VIF > 4 were considered collinear and were restricted from occurring in the same model together during model selection (Dyson et al. 2019). We assessed model fit by visualizing the receiver operating characteristic curve (ROC) and calculating area under the curve (AUC) for all top models.

In stage one, each individual variable was ranked individually in linear and quadratic forms and compared to a null model using Akaike's Information Criterion adjusted for small sample size (AIC_c) and the top model was selected based on the lowest AIC_c score. If the top models did not include the null ($\Delta AIC_c > 4$) this variable moved on to stage two, otherwise it was discarded. In stage two, we ranked all combinations of predictors selected in stage one and compared models to a null model using AIC_c. We present all models within 4 ΔAIC_c scores of the top model, cumulative weight of evidence ($\sum \omega_i$) for each predictor across all models, and parameter estimates with 85% confidence intervals (Arnold 2010). This two-stage analysis was performed on all nests monitored across Suisun and the subset of nests that were monitored on the main GIWA property only. Model selection was performed using the model.sel function in package "MuMIn" (Bartoń 2020). All analyses were performed in Program R (version 3.6.3; R Core Team 2020).

2.6 Macrohabitat Nest Site Selection

For macrohabitat nest site selection a new set of random sites was randomly generated in a geographic information system (GIS, ArcMap 10.7.1, ESRI, Redwood City, CA) such that random sites paired to nest sites were > 50 m away to differentiate from microhabitat random sites described above. For all nest and random site locations the following straight-line distances were calculated for each site by year: distance to nearest harrier nest, distance to the nearest road (paved, gravel, or levee), distance to nearest manmade structure (homes, outbuildings), distance to nearest tree, and distance to nearest water. We also isolated vegetation species of interest from the Suisun Vegetation Map (Boul et al. 2018) and calculated distance to each nest and random site. Vegetation species that were potential management issues in Suisun but were observed as either selected habitat for nest sites, Common Reed (*Phragmites australis*) and California Rose (*Rosa californica*), or avoided habitat for nest sites, Coyote Bush (*Baccharis pilularis*), Quail Bush (*Atriplex lentiformis*) and Willow (*Salix* spp.), were chosen. Individual vegetation species distances were also combined into two variables as selected habitat ("Nestable") and avoided habitat ("Unnestable"). Additionally, we calculated distance to nearest tree-nesting raptor (Red-tailed Hawk, *Buteo jamaicensis*; Swainson's Hawk, *Buteo swainsoni*; or Great Horned Owl, *Bubo virginianus*) or Common Raven (*Corvus corax*) nest, and distance to nearest ATV track for harrier nests on GIWA only because these two features were only recorded there. The water layers were digitized using the same April multispectral satellite imagery layers described above for each year (2017-2019).

We used conditional logistic regression as described above but used a three-stage approach instead of a two-stage approach. Stage one was identical to microhabitat nest site selection. In stage two, we then tested predictor variables from stage one in three different model classes: landscape features (distance to water, trees, structures, and roads), vegetation (distance to specific vegetation species of interest: Common Reed, California Rose, Coyote Bush, Quail Bush, Willow, or Nestable Vegetation, and Unnestable Vegetation), habitat type (managed marsh, tidal marsh, upland), small mammal (small mammal density at 1 km^2 and 5 km^2), and competition (distance to nearest harrier nest and raptor/raven stick nest). All combinations of predictors in each model class were compared to a null model using AIC_c and top models with the lowest AIC_c score from each model class moved on to stage three. In stage three, all combinations of top model classes from stage two were compared to a null model and ranked using AIC_c. We present all models within 4 ΔAIC_c scores of the top model, cumulative weight of evidence ($\sum \omega_i$) for each predictor across all models, and parameter estimates with 85% confidence intervals (Arnold 2010). This three-stage analysis was performed on all nests monitored across Suisun and the subset of nests that were monitored on GIWA only. The competition model class was only tested on the GIWA nests because raptor/raven stick nests were only monitored here and distances between harrier nests are most relevant here because GIWA represents one large contiguous area. Distance to ATV tracks was also included in the landscape features model class for GIWA only nests because ATV tracks were only recorded here.

2.7 Home Range Nest Site Habitat Selection

Home ranges were calculated using dynamic Brownian bridge movement models (dBBMM). Movement models have an advantage over traditional home range estimators, like kernel density estimators (KDE), such that they model the home range of each animal represented by a utilization distribution (UD) based on their movement path (i.e., temporally dependent locations), rather than all locations within the home range independent of their temporal correlation (Horne et al. 2007, Byrne et al. 2014). Further, KDE do not perform well on large GPS datasets and results can vary drastically based on the smoothing parameter (h) used (Fischer et al. 2013, Byrne et al. 2014).

Brownian bridge movement models (BBMM) have three main requirements: 1) temporally dependent locations, 2) error associated with GPS locations, and 3) a grid cell size for the output UD. There are also two main assumptions: 1) location errors are normally distributed, and 2) movement between locations is random (Horne et al. 2007). The first assumption is met by utilizing GPS data, which typically displays normally distributed error around locations. By using short time-interval fixes (i.e., 2-3 hours or less), this ensures movement between locations is random. Further, successive locations do not require equal time-interval fixes, which allows for some variation in temporal resolution of the data, a common problem with any animal movement data.

BBMM work by accounting for the tortuosity of the movement path (i.e., the behavior of the animal) by calculating a parameter known as the motion variance (σ^2) based on the time and distance between successive locations. In BBMM, motion variance is held constant across the entire movement path (Horne et al. 2007). However, dBBMM improves upon the BBMM by allowing σ^2 to vary across the movement path by calculating a new σ^2 after each time step, resulting in a more accurate representation of the animal's UD (Byrne et al. 2014), with all other requirements and assumptions remaining the same. dBBMM home ranges were calculated using the "move" package (Kranstauber et al. 2019) in program R (version 3.6.3; R Core Team 2020).

The resulting UD contains probabilities of occurrence associated with each grid cell that is then overlaid onto a raster land cover layer with the same grid cell size. The two layers are multiplied, resulting in a probability of land cover use by each grid cell. These probabilities are then summed to derive the overall probability of land cover use by each land cover class within each UD. This procedure is similar to calculating probability of habitat use from UDs calculated from KDE described by Millspaugh and colleagues (2006). We used the 2016 National Land Cover Database raster layer (Wickham et al. 2021) containing the following land cover classes: Barren, Developed, Forest, Herbaceous (Grassland), Planted/Cultivated, Shrubland, and Wetlands. Within each land cover class exist multiple layers representing different levels of land cover intensity or classification. For example, Herbaceous contains layers for Grassland/Herbaceous, Sedge/Herbaceous, Lichens, and Moss. We summed all layers within each land cover class for ease of analysis and interpretation. The land cover raster was clipped to the extent of Suisun prior to analysis. We performed a post-hoc Tukey's HSD analysis on the landcover probabilities across all habitat types for all birds to test for significant differences in probability of landcover use.

Dates for locations used in breeding home range estimation began 24 hrs after transmitter deployment for females captured at the nest to allow for acclimation to transmitters and resumption of normal behavior, or when incubation began for one female that was captured and marked in the winter prior to the breeding season and the exact start of incubation could be determined based on transmitter locations. End dates for locations were up to six weeks post-fledge, which is the amount of time females were observed still provisioning fledglings in the nest area and fledglings were still using the nest site to roost (unpublished data), or when the adult female left the nest area and did not return for more than 24 hrs. We also calculated the mean distance between locations for each day to visualize how female home range expands across the breeding season.

3. Results

3.1 Nest Surveys and Access

From 2017–2019 we found and monitored 77 harrier nests in Suisun, 53 of which occurred on GIWA. We found 13 nests in 2017, 30 nests in 2018, and 34 nests in 2019. More nests were found in 2018 and 2019 likely because we increased our search effort by 20–30 km^2 and increased our survey team size from two people (often paired) in 2017 to three people (often independent) in 2018 and 2019. However, extensive winter flooding in 2017 also reduced available nesting habitat for ground-nesting birds in the spring and reduced our access to large areas of Suisun for nest searching. Nest density across searched areas within Suisun was approximately 0.30, 0.48, and 0.47 nests/km^2 across all three years, respectively. On GIWA only, nest density was approximately 0.25, 0.58, and 0.50 nests/km^2 across all three years, respectively.

Harrier nests were generally found in tall, dense cover either directly on the ground or slightly elevated from the ground. The average height for all harrier nests was 23.9 cm from the ground to the top of the nest (Table 2.1). We did not record the distance from the ground to the bottom of the nest if it was elevated. Nests had a slightly oval shape, with average length (45.0 cm) larger than average width (38.5 cm, Table 2.1). Live vegetation height (103.2 cm) and cover (61.9%) was greater than dead vegetation height (58.8 cm) and cover (8.9%), as well as residual vegetation height (68.88 cm) and cover (29.1%), on average (Table 2.1). Overall, the average height of vegetation at the nest was 82.1 cm. Average visual obstruction across all four cardinal directions was 93.3 cm (Table 2.1). Most vegetation species documented at nest sites were emergent graminoids (55.6%), followed by forbs (18.7%) and terrestrial graminoids (18.1%) in nearly equal proportion, and shrubs (7.3%; Table 2.1). Nest sites contained more Common Reed and California Rose than random sites both across Suisun and on GIWA (Table 2.1).

Table 2.1. Summary statistics of microhabitat variables used in conditional logistic regression analysis for all Northern Harrier nest sites (n = 77) and paired random sites across Suisun Marsh and nest sites (n = 53) and paired random sites on Grizzly Island Wildlife Area (GIWA) only (2017–2019). Nest characteristics, vegetation height, and visual obstruction are reported as mean height in cm (sd). Vegetation cover, vegetation functional group, and vegetation species are reported as proportion (sd) of each cover vegetation (live, dead, residual), functional group vegetation (emergent, terrestrial, forb, shrub, unidentified), and species (Common Reed and California Rose) present at each nest and random site, respectively.

Variable	**All Nests**	**Random**	**GIWA Nests**	**GIWA Random**
Nest Characteristics				
Nest Height	23.92 (14.54)	N/A	19.24 (13.70)	N/A
Nest Length	44.95 (12.39)	N/A	43.91 (13.51)	N/A
Nest Width	38.50 (9.31)	N/A	37.50 (10.50)	N/A
Vegetation Heights				
Live Height	103.19 (36.90)	91.44 (50.14)	95.35 (40.07)	81.18 (49.69)
Dead Height	58.79 (23.51)	54.91 (30.43)	55.66 (23.53)	42.71 (21.64)
Residual Height	68.88 (31.05)	64.36 (36.22)	68.87 (34.99)	61.64 (36.10)
Average Height	82.10 (26.78)	74.19 (38.01)	76.92 (28.69)	66.80 (38.18)
Tallest Vegetation Height	136.58 (39.31)	128.37 (62.73)	127.91 (42.03)	110.47 (55.31)
Visual Obstruction				
N	86.76 (57.84)	80.45 (62.61)	83.21 (64.87)	68.82 (61.0)
E	92.37 (60.40)	72.56 (63.06)	84.52 (64.08)	59.67 (63.26)
S	96.41 (59.75)	75.88 (59.87)	88.16 (66.77)	64.86 (63.04)
W	94.87 (54.59)	77.86 (60.88)	87.12 (60.91)	62.74 (52.77)
Average	93.31 (53.55)	76.69 (58.63)	85.51 (60.49)	64.02 (57.53)
Vegetation Cover				
Live Cover	61.87 (23.52)	57.94 (28.96)	63.19 (25.82)	60.18 (29.39)
Dead Cover	8.90 (17.29)	10.64 (19.58)	10.57 (19.16)	10.92 (19.50)
Residual Cover	29.09 (22.72)	28.58 (27.01)	26.11 (22.37)	28.73 (27.73)

Vegetation Functional Group				
Emergent Graminoid	55.61 (43.92)	43.29 (45.70)	44.68 (44.78)	32.62 (43.79)
Terrestrial Graminoid	18.05 (36.45)	30.11 (39.59)	25.62 (41.80)	37.67 (42.71)
Forb	18.70 (31.73)	21.91 (34.06)	18.77 (32.22)	23.02 (34.78)
Shrub	7.26 (20.65)	4.35 (18.38)	10.55 (24.25)	6.32 (21.93)
Vegetation Species				
Common Reed	14.62 (35.03)	9.68 (29.11)	20.64 (40.73)	13.28 (34.16)
California Rose	7.26 (20.65)	1.33 (10.83)	10.55 (24.25)	1.93 (13.05)

3.2 Capture and Transmitter Deployment

We captured and marked 10 adult females during the breeding seasons; five females in 2018 were equipped with Ecotone Crex transmitters; five females in 2019 were equipped with Ornitela OrniTrack-10 transmitters. Due to transmitter failure on one female, we recorded locations from only four females in 2018. And in 2019, we recorded locations from all five females plus a sixth female that was captured and marked in the previous winter and remained in Suisun to breed. We collected a total of 12,886 locations, with an average of 1,288.6 locations per female during the breeding seasons (Table 2.2).

Table 2.2. Transmitter type, date deployed, location interval, nesting period used to develop home ranges, and number of nesting period locations for adult breeding females in Suisun Marsh across two breeding seasons (2018–2019).

Bird ID	Transmitter Type	Date Deployed	Interval	Nesting Period	# Locations
SIMP 01	Ecotone	2 June 2018	1 hr	4 June–22 July	605
SIMP 02	Ecotone	17 May 2018	1 hr–2 hr	18 May–25 July	1036
SIMP 07	Ecotone	10 June 2018	1 hr–2 hr	11 May–24 July	282
SIMP 10	Ecotone	17 June 2018	1 hr	18 May–13 July	420
NOHA 626	Ornitela	29 May 2019	30 min	30 May–3 August	2267
NOHA 627	Ornitela	1 June 2019	30 min–2 hr	2 June–27 July	1820
NOHA 628	Ornitela	2 June 2019	5 min–30 min	3 June–23 July	1556
NOHA 629	Ornitela	2 June 2019	30 min–2 hr	3 June–7 August	1856
NOHA 630	Ornitela	14 June 2019	30 min–1 hr	15 June–26 July	1233
NOHA 30.1	Ornitela	23 March 2019	30 min–1 hr	15 June–14 August	1811
				Total	*12886*

3.3 Small Mammal Trapping and Density Estimates

We captured six species of small mammals for a total of 641 individual small mammals across 924 total captures, though species composition and dominance varied each year (Table 2.3). Harvest mice (Western and Salt Marsh Harvest Mice combined) were the most common small mammals captured (69.4%) and were the most common species captured in 2017 and 2019, but the second most common in 2018 (Table 2.3). House Mice were the second most common species captured on average (27.6%), and were the most common species captured in 2018, but the second most common in 2017 and 2019 (Table 2.3). All other species combined (California Voles, *Rattus* spp. and Deer Mice) comprised only 3% of average captures. California Voles were the least common species captured in 2017 and were captured only slightly more often than *Rattus* spp. and Deer Mice in 2018 and 2019, but only by a few individuals each year (Table 2.3). Small mammal populations overall were very low in 2017, high in 2018, and intermediate in 2019 (Table 2.3).

Density and abundance estimates from the oSCR analysis followed a similar pattern to capture statistics, with Harvest Mice being the most dense (360.3 km^{-2}) and abundant (40,885.9 individuals) on average across all years (Table 2.4). However, Harvest Mice were the most dense and abundant species in 2017 and 2018, but the second most in 2019 (Table 2.4). Whereas House Mice were the second most dense (75.3 km^{-2}) and abundant (7,555.7 individuals) on average across years, and the most dense and abundant species in 2019 only (Table 2.4). Across all small mammals, the density estimate (292.94 km^{-2}) was highest in 2017, while abundance estimate (36726.4 individuals) was highest in 2018 (Table 2.4).

Table 2.3. Summary of small mammal individual captures (*n*), recaptures, total captures, and proportion (%) of all captures across all spring trapping periods in Suisun Marsh, CA from 2017–2019. Total trap nights for each year were: 719 (2017), 2,497 (2018), and 2,489 (2019).

Species	**Year**	***n***	**Recaptures**	**Total Captures**	**% Captures**
House Mouse	2017	2	3	5	3.9
	2018	244	78	322	54.8
	2019	35	6	41	24.1
Harvest Mouse[1]	2017	47	28	75	92.2
	2018	191	105	296	42.9
	2019	106	52	158	73.1
California Vole	2017	0	0	0	0.0
	2018	5	1	6	1.1
	2019	2	2	4	1.4
Rattus spp.[2]	2017	1	0	1	2.0
	2018	3	0	3	0.7
	2019	0	0	0	0.0
Deer Mouse	2017	1	1	2	2.0
	2018	2	7	9	0.4
	2019	2	0	2	1.4
Total Small Mammals	*2017*	*51*	*32*	*83*	*100*
	2018	*445*	*191*	*636*	*100*
	2019	*145*	*60*	*205*	*100*
	Total	*641*	*283*	*924*	*100*

[1] Includes both Western (*Reithrodontomys megalotis*) and Salt Marsh Harvest Mice (*Reithrodontomys raviventris*).

[2] Rats were not identified to species but include either Norway Rat (*Rattus norvegicus*) or Roof Rat (*Rattus rattus*).

Table 2.4. Summary statistics from the spatial capture–recapture models fitted to the spring season for three years (2017–2019) of small mammal trapping in Suisun Marsh, CA. Species include: House Mouse (*Mus musculus),* Harvest Mouse (Salt Marsh Harvest Mouse, *Reithrodontomys raviventris*, and Western Harvest Mouse, *Reithrodontomys megalotis*, combined), and all small mammals (House Mice, Harvest Mice, Deer Mice, *Peromyscus maniculatus*, Rats, *Rattus* spp., and California Voles, *Microtus californicus*). Estimates were modeled with Normalized Difference Vegetation Index (NDVI) at 250 m grid cell resolution as the predictor variable. Parameter estimates represent mean density (*D*) km^{-2}, and total abundance (*N*) across the entire state space including standard error (SE) and 95% confidence interval (CI).

		Density (*D*)			**Abundance (*N*)**		
Species	**Year**	**Estimate**	**SE**	**95% CI**	**Estimate**	**SE**	**95% CI**
House Mouse	2017	14.96	13.50	2.72–98.50	455.97	411.38	82.93–2998.58
	2018	97.74	23.19	61.48–155.83	15287.94	3626.69	9616.97–24374.43
	2019	113.07	55.24	43.90–298.21	6923.12	3382.27	2688.18–18259.12
Harvest Mouse	2017	307.69	116.10	148.97–654.12	12504.69	4718.24	6053.96–26583.24
	2018	678.95	100.12	509.34–908.07	98612.89	14541.45	73978.25–131890.03
	2019	94.24	21.96	60.38–150.81	11540.14	2689.66	7394.50–1846.36
All Small Mammals	2017	292.94	105.83	145.89–601.47	11904.94	4300.99	5929.08–24443.65
	2018	219.15	30.45	167.03–287.97	36726.43	5102.40	27992.76–48259.99
	2019	148.02	30.79	99.31–224.60	18126.93	3770.29	12162.11–27505.06

3.4. Microhabitat Nest Site Selection

The top model that predicted microhabitat for nest site selection across Suisun included the quadratic form for average vegetation height, proportion rose, and proportion terrestrial graminoids (Table 2.5). The highest probability of nest site selection was at sites with 80-cm tall vegetation (P = 0.62, β = –0.53, 85% CI = –0.84 to –0.27) and 30-55% rose present at the nest (P = 1.00, β = –1.01, 85% CI = –2.14 to –0.33; Fig. 2.4). Sites with 50% terrestrial graminoids relative to random sites had the lowest probability of nest site selection (P = 0.46, β = 1.22, 85% CI = 0.58–1.92), with harriers exhibiting stronger selection for nest sites with a lot or very little terrestrial graminoids present (Fig. 2.4). The cumulative weight of evidence for average vegetation height, proportion rose, and proportion terrestrial graminoids were all ~ 0.90 (Table 2.6). Proportion live vegetation had a cumulative weight of evidence of 0.44 (Table 2.6) but was not included in the top model.

The top model that predicted microhabitat nest site selection on GIWA only included quadratic forms of average vegetation height and proportion rose (Table 2.5). Sites with an average vegetation height of 100 cm (P = 0.91, β = –0.35, 85% CI = –0.63 to –0.14) and with 30–55% rose present at the nest (P = 1.00, β = –0.88, 85% CI = –1.88 to –0.29) had the highest probability of nest site selection (Fig. 2.5). The cumulative weight of evidence for average vegetation height and proportion rose was 1.00 and 0.95, respectively (Table 2.6). No other variables were included in the GIWA-only models.

Table 2.5. Microhabitat harrier nest site selection for conditional logistic regression model sets at two different spatial scales: Suisun Marsh and Grizzly Island Wildlife Area (GIWA) in Suisun Marsh, CA from 2017-2019. Variables across all models represent vegetation measurements recorded at nest and random sites. Models are ranked using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) based on the number of parameters (K) in the model, –2 × log likelihood (L), and Akaike weights (ω_i). Models within ≤ 4 ΔAIC_c scores are presented.

Spatial Scale	**Model**	K	**–2(L)**	AIC_c	ΔAIC_c	ω_i
Suisun	Height^2 + % Rose^2 + % Terrestrial^2	6	–88.93	194.85	0.00	0.46
	Height^2 + % Rose^2 + % Terrestrial^2 + % Live^2	8	–87.02	195.58	0.72	0.32
	Height^2 + % Terrestrial^2 + % Live^2	6	–90.91	198.81	3.96	0.06
GIWA	Height^2 + % Rose^2	4	–57.25	127.43	0.00	0.95

Table 2.6. Cumulative AIC_c weights of evidence ($\sum \omega_i$) of all microhabitat nest site selection model parameters for harrier nests at different spatial scales in Suisun Marsh, CA from 2017-2019.

Spatial Scale	**Model and Model Parameters**	$\sum \omega_i$
Suisun	% Terrestrial	0.94
	Height	0.94
	% Rose	0.88
	% Live	0.44
	Visual Obstruction	0.02
GIWA	Height	1.00
	% Rose	0.95

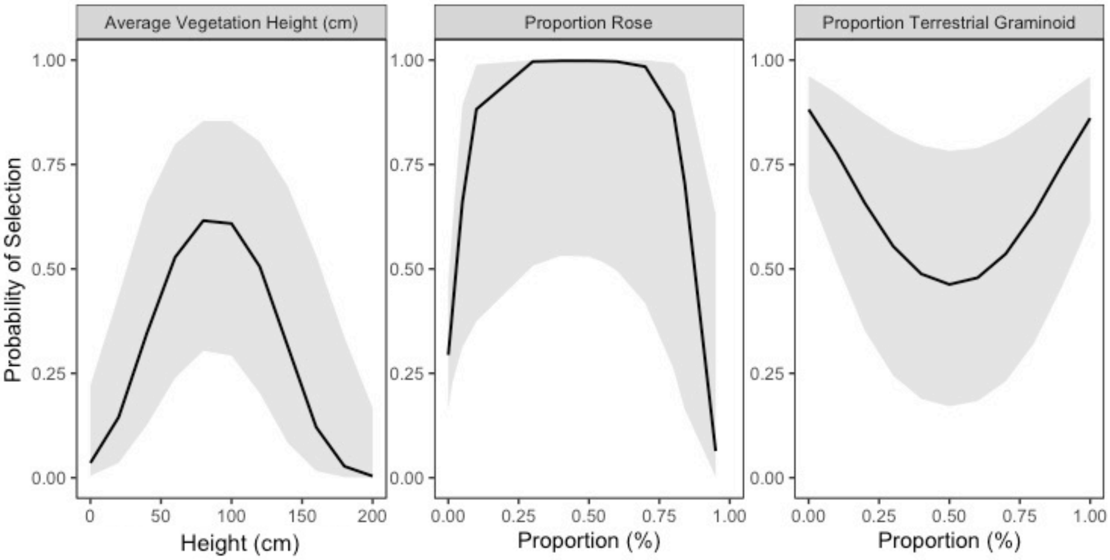

Figure 2.4. Effect plots representing parameters from the top global model for microhabitat nest site selection for all harrier nests (n = 77) across Suisun Marsh, CA from 2017–2019. Shaded areas represent 85% CI.

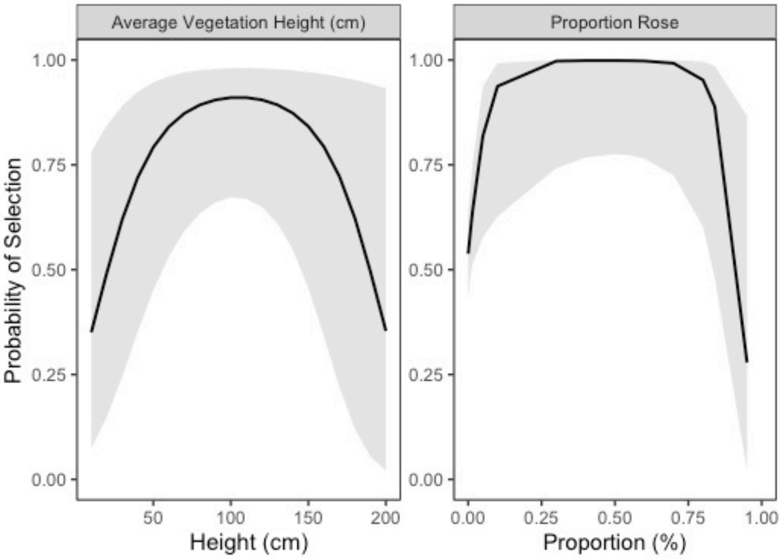

Figure 2.5. Effect plots representing parameters from the top global model for microhabitat nest site selection for harrier nests (n = 53) on Grizzly Island Wildlife Area only in Suisun Marsh, CA from 2017–2019. Shaded areas represent 85% CI.

3.5 Macrohabitat Nest Site Selection

Across Suisun, 45% of nests (66% on GIWA) occurred in managed marshes, with 29% in tidal marsh (no tidal marsh on GIWA), and 26% in upland fields (34% on GIWA, Table 2.7). We measured distances to 13 landscape, vegetation, and competition features in a GIS for all harrier nests and random sites (Table 2.7). The top landscape features model that predicted nest site selection across Suisun included the quadratic form of distance to water (Table 2.8, Fig. 2.6 A) with a cumulative weight of evidence of 0.98 (Table 2.9). The top vegetation model that predicted nest site selection included only the quadratic form of distance to unnestable vegetation (Table 2.8, Fig. 2.6 B) with a cumulative weight of evidence of 0.99 (Table 2.9). The global model included both variables above (Table 2.8) with cumulative weights of evidence for both variables ≥ 0.96 (Table 2.9). The probability of selection for distance to water was highest at 110-140 m from water (P = 0.81, β = –0.31, 85% CI = –0.51 to –0.12), and 1500 m from unnestable vegetation (P = 0.74, β = –0.71, 85% CI = –1.20 to –0.33; Fig. 2.7) in the global model.

The top landscape features model for GIWA nests included the quadratic form of distance to water and the linear form of distance to ATV tracks (Table 2.8, Fig. 2.8 A). The probability of selection for distance to water was highest at 110 m (P = 0.71, β = –0.33, 85% CI = –0.59 to –0.08). Harriers selected nest sites that were farther away from ATV tracks compared to random sites (β = 0.47, 85% CI = 0.14–0.83). The cumulative weights of evidence for distance to ATV tracks and water was 0.81 and 0.76, respectively (Table 2.9). The top model for vegetation included the quadratic forms of distance to rose and quail bush (Table 2.8, Fig. 2.8 B). The probability of nest site selection was highest closer to rose (P = 0.65, β = 0.72, 85% CI = 0.39–1.06), but farther away from quail bush (P = 0.99, β = 0.99, 85% CI = 0.50–1.52) The cumulative weight of evidence for distance to rose and quail bush was 0.98, respectively (Table 9). In the competition model, harriers selected nest sites closer to other harrier nests compared to random sites ($\beta = -0.53$, 85% CI = –0.88 to –0.22; Table 2.8, Fig. 2.9) with distance to other competitor nests not included in the top model. Lastly, the top global model was the vegetation model from above, with distance to rose ($\beta = -1.36$, 85% CI = 0.39 to 1.06) and quail bush ($\beta =$ 0.99, 85% CI = 0.50 to 1.52; Table 2.8, Fig 2.10) as the top predictors for net site selection on GIWA, though the second competing model also included distance to harrier nests with high model uncertainty (Table 2.8). The cumulative weights of evidence for both rose and quail bush was 1.00, respectively, with low support for any other predictors (Table 2.9). We found no effect of habitat type or small mammal density on nest site selection.

Table 2.7. Summary statistics of macrohabitat variables used in conditional logistic regression analysis for all Northern Harrier nest sites (n = 77) and paired random sites across Suisun Marsh, and for nest sites (n = 53) and paired random sites on Grizzly Island Wildlife Area (GIWA) only. Habitat type represents the proportion and number (n) of nests within each habitat. GIS Distance (m) represents the mean (sd) of GIS-derived distances to each variable from nests and random sites. Distances to harrier nests, stick nests, and ATV tracks were calculated for Grizzly Island Wildlife Area (GIWA) only.

Variable	**All Nests**	**All Random**	**GIWA Nests**	**GIWA Random**
Habitat Type				
Managed Marsh	45.45 (35)	59.74 (46)	66.01 (35)	71.70 (38)
Tidal Marsh	28.57 (22)	19.48 (15)	0.00 (0)	3.77 (2)
Upland Field	25.97 (20)	20.78 (16)	33.96 (18)	24.53 (13)
GIS Distances				
Harrier Nests	N/A	N/A	605.66 (483.49)	851.19 (539.38)
Active Stick Nests	N/A	N/A	1514.10 (881.90)	1500.66 (987.43)
Roads	81.31 (84.91)	75.49 (69.70)	74.71 (83.90)	57.54 (56.10)
Structures	1027.50 (642.62)	987.10 (554.51)	1244.97 (640.85)	1084.26 (592.42)
Trees	454.73 (279.35)	571.05 (362.93)	460.08 (249.71)	570.25 (390.09)
Water	58.52 (49.18)	49.57 (48.40)	65.70 (54.04)	42.79 (49.90)
ATV Tracks	N/A	N/A	744.12 (895.55)	381.23 (541.27)
Common Reed	144.03 (151.13)	140.91 (170.36)	87.90 (102.04)	108.17 (108.66)
California Rose	1004.79 (1094.25)	1254.43 (1157.28)	665.11 (780.52)	835.08 (624.85)
Coyote Bush	1178.55 (1492.02)	1298.90 (1864.31)	595.58 (388.94)	525.75 (412.53)
Quail Bush	3214.58 (2447.35)	2657.59 (2342.01)	2226.40 (1594.49)	1515.43 (1031.54)
Willow	12893.45 (3330.69)	11790.05 (3225.78)	13087.26 (2738.75)	11435.05 (2360.18)
Nestable	124.12 (152.59)	135.27 (163.32)	65.75 (102.47)	102.13 (104.36)
Unnestable	698.85 (790.94)	1203.78 (1760.17)	434.89 (371.91)	455.10 (388.14)

Table 2.8. Macrohabitat nest site selection for conditional logistic regression model sets at two different spatial scales: Suisun Marsh and Grizzly Island Wildlife Area (GIWA) in Suisun Marsh, CA from 2017-2019. Variables across all models represent GIS-derived nearest distance (m) to nest and random sites. Model sets include nearest distance to variables selected after initial testing of individual variables to the null. Full variables by model class include: Features (trees, water, structures, roads, and ATV tracks (GIWA only)), Vegetation (coyote bush, quail bush, phragmites, and rose), and Competition (harrier nests and stick nests of raptor and corvid species). Global models represent all combinations of top models from each model class (Features, Vegetation, Competition). Models are ranked using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) based on the number of parameters (*K*) in the model, –2 × log likelihood (*L*), and Akaike weights (ω_i). Models within ≤ 4 ΔAIC_c scores are presented.

Spatial Scale and Model Class	**Model**	***K***	**–2(*L*)**	**AIC_c**	**ΔAIC_c**	**ω_i**
Suisun						
Landscape	Water^2	2	–100.85	209.97	0.00	0.88
Vegetation	Unnestable^{2a}	2	–99.29	206.85	0.00	0.97
Global	Water^2 + Unnestable^{2a}	4	–93.91	200.40	0.00	0.95
GIWA						
Landscape	Water^2 + ATV Tracks	3	–66.82	144.23	0.00	0.60
Vegetation	Rose^2 + Quail^2	4	–59.66	132.16	0.00	0.96
Competition	Harrier Nests	1	–70.35	146.94	0.00	0.48
	Harrier Nests^2	2	–69.34	147.07	0.13	0.45
Global	Rose^2 + Quail^2	4	-59.66	132.16	0.00	0.52
	Rose^2 + Quail^2 + Harrier Nests	5	-58.79	132.71	0.55	0.40

[a] Unnestable vegetation includes distances to shrub habitat not suitable for nesting (coyote bush, quail bush, and willow).

Table 2.9. Cumulative AIC_c weights of evidence ($\sum \omega_i$) of all macrohabitat nest site selection model parameters for harrier nests at different spatial scales in Suisun Marsh, CA from 2017-2019.

Spatial Scale and Model Class	**Model Parameters**	$\sum \omega_i$
Suisun		
Landscape	Water	0.98
Vegetation	Unnestable[a]	0.99
Global	Unnestable[a]	0.99
	Water	0.96
GIWA		
Landscape	ATV Tracks	0.81
	Water	0.76
Vegetation	Rose	0.98
	Quail	0.98
Competition	Harrier Nests	0.94
Global	Rose	1.00
	Quail	1.00
	Harrier Nests	0.42
	Water	0.08
	ATV Tracks	0.08

[a] Unnestable vegetation includes distances to shrub habitat not suitable for nesting (coyote bush, quail bush, and willow).

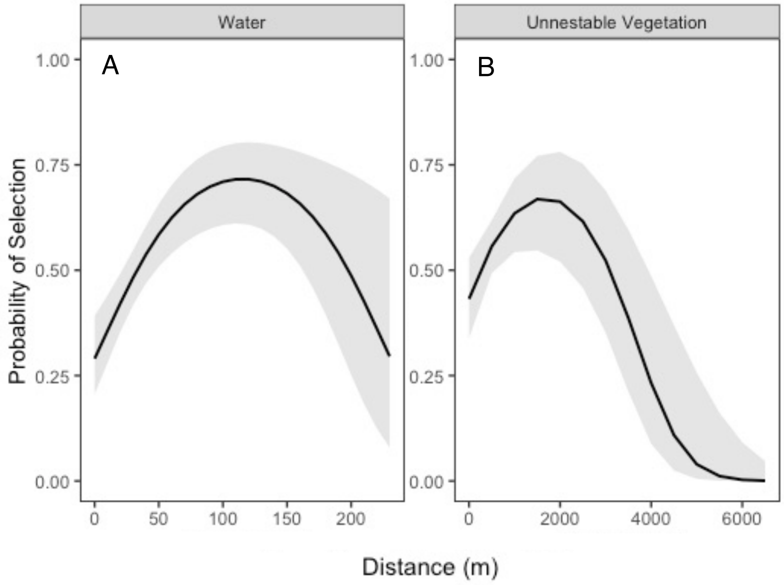

Figure 2.6. Effect plots representing parameters from the top landscape (A) and vegetation (B) models for macrohabitat nest site selection for all harrier nests (n = 77) across Suisun Marsh, CA from 2017–2019. Shaded areas represent 85% CI.

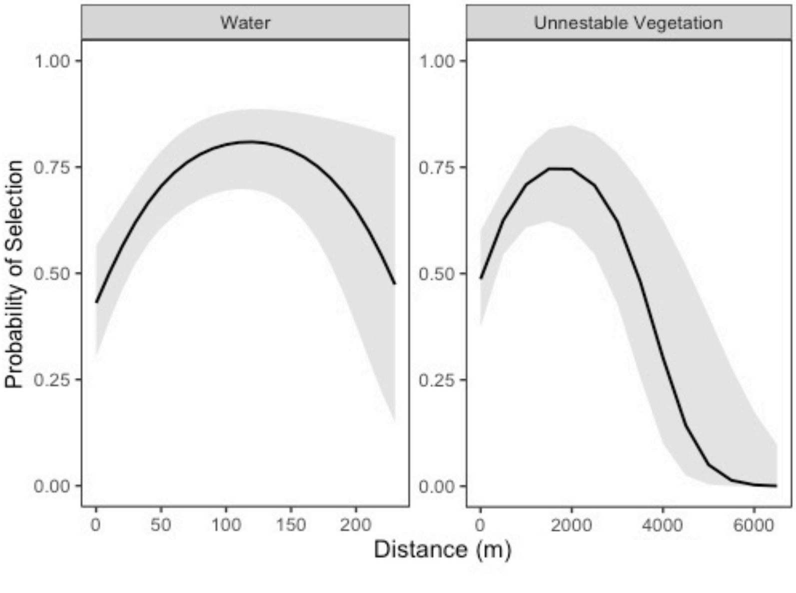

Figure 2.7. Effect plots representing parameters from the top global model for macrohabitat nest site selection for all harrier nests (n = 77) across Suisun Marsh, CA from 2017–2019. Shaded areas represent 85% CI.

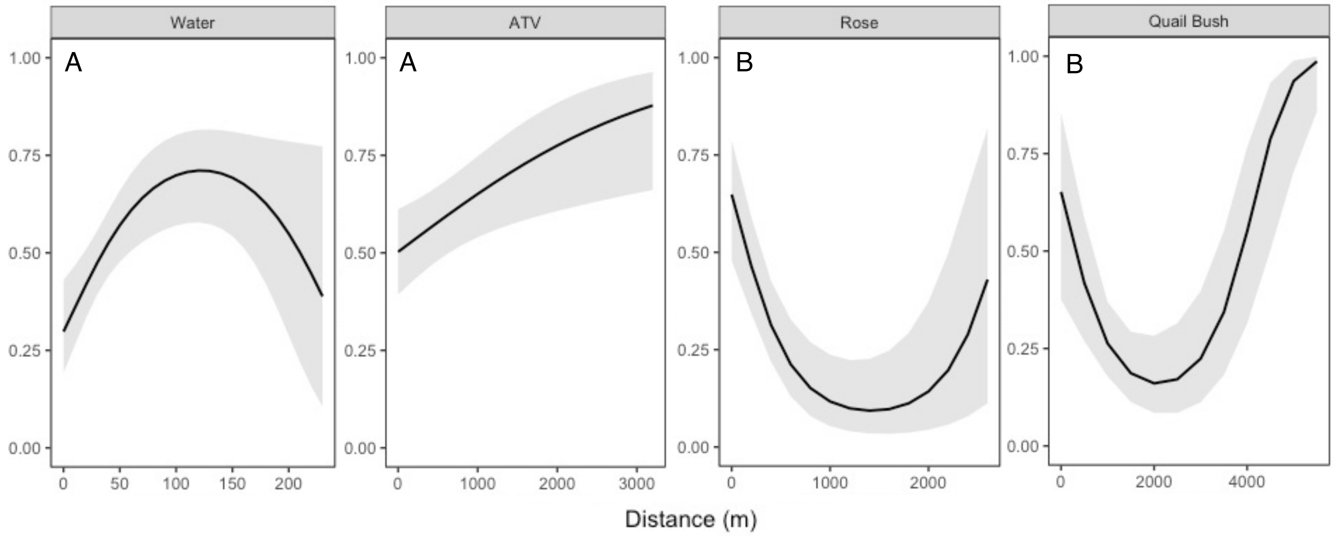

Figure 2.8. Effect plots representing the parameters from the top landscape (A) and vegetation (B) models for macrohabitat nest site selection for harrier nests (n = 53) on Grizzly Island Wildlife Area only in Suisun Marsh, CA from 2017–2019. Shaded areas represent 85% CI.

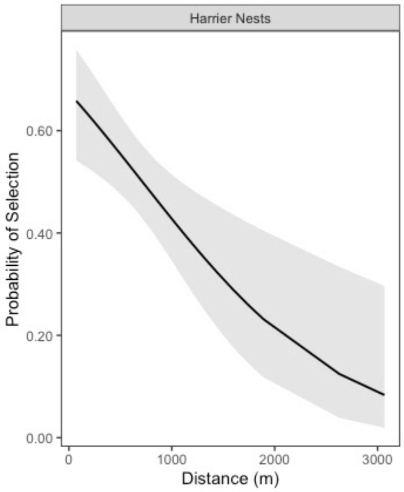

Figure 2.9. Effect plots representing the parameters from the top competition model for macrohabitat nest site selection for harrier nests (n = 53) on Grizzly Island Wildlife Area only in Suisun Marsh, CA from 2017–2019. Shaded areas represent 85% CI.

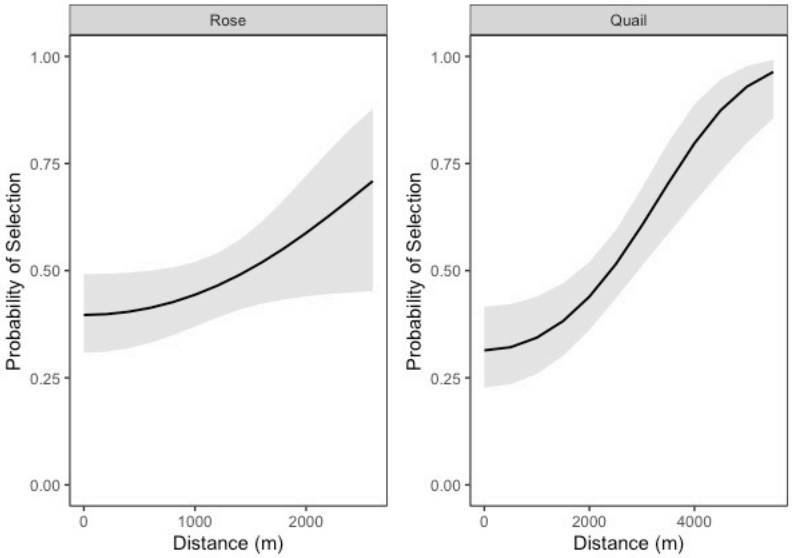

Figure 2.10. Effect plots representing the parameters from the top global model for macrohabitat nest site selection for harrier nests (n = 53) on Grizzly Island Wildlife Area only in Suisun Marsh, CA from 2017–2019. Shaded areas represent 85% CI.

3.6 Home Range Nest Site Habitat Selection

We calculated dBBMM breeding home ranges for 10 adult breeding females captured in 2018 and 2019 (Fig. 2.11). The average 95% home range size for all 10 females was 5.32 km^2 (range: 0.76–11.02 km^2), with a 50% core use area of 0.20 km^2 (range: 0.005–0.70 km^2). On average, the land cover class with the highest probability of use in the 95% home range was wetland vegetation (P = 0.73, 95% CI = 0.56–0.89) followed by open water (P = 0.13, 95% CI = –0.02 to 0.27) and grassland vegetation (P = 0.11, 95% CI = 0.42–0.18). All other land cover classes represented less than 3% probability of use each (Fig. 2.12). Only probability of wetland habitat use was significantly different than all other habitat types based on the Tukey's HSD analysis ($p < 0.001$). There were no other significant pairwise differences between habitat types.

Overall, female home range size expanded across the breeding season as mean distance between locations increased for eight of nine females across the breeding seasons in 2018 (Fig. 2.13) and 2019 (Fig. 2.14, Table 2.10). Mean distance traveled to and from the nest site increased by 390 m from the first 7 days to the last 7 days of the breeding season (Table 2.10). One female (NOHA 07) was excluded from this analysis because of missing location data across the nesting period.

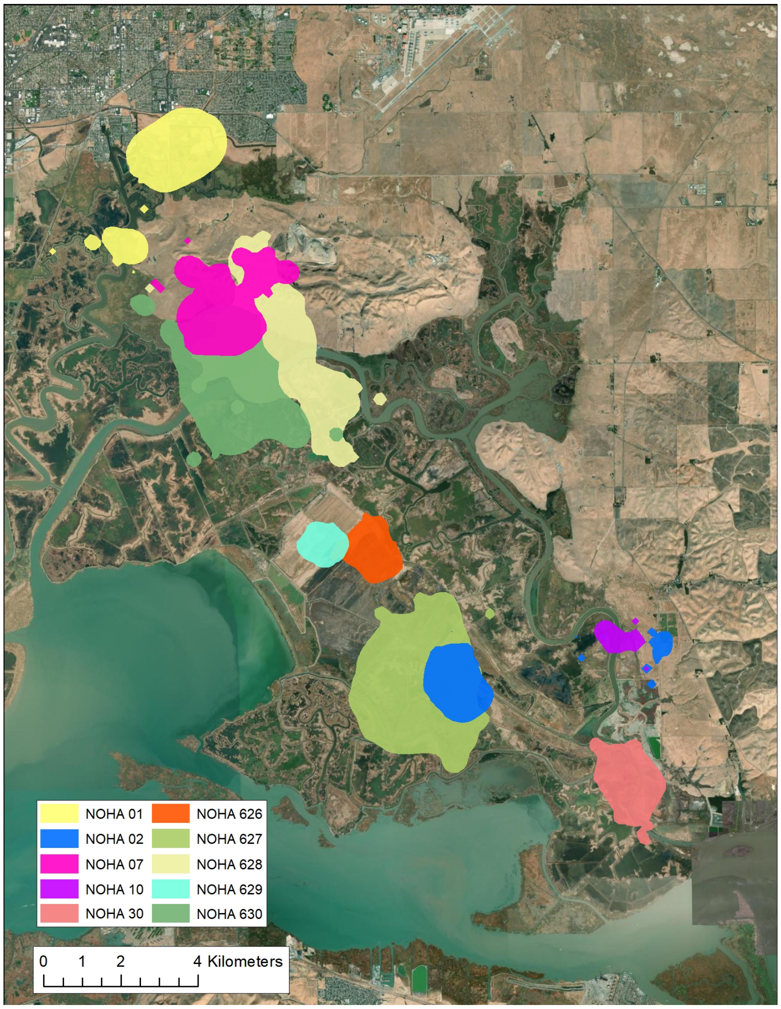

Figure 2.11. Map of 95% dynamic Brownian bridge movement model (dBBMM) breeding home ranges for 10 adult female Northern Harriers (2018–2019) in Suisun Marsh, CA.

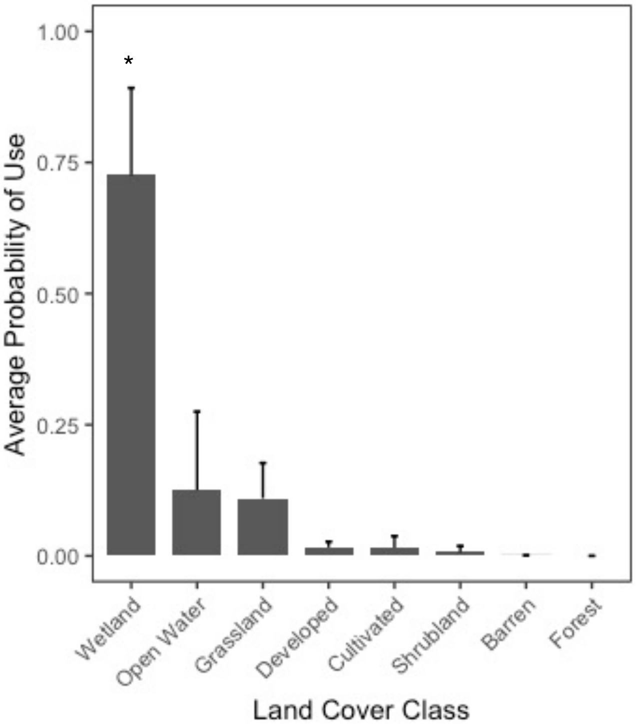

Figure 2.12. Average probability of use (+ 95% CI) by land cover class within the 95% dynamic Brownian bridge movement model home range for adult breeding northern harrier females (n = 10) in Suisun Marsh, CA (2018–2019). Asterisk (*) represents significant difference between wetland habitat and all other habitat types based on Tukey's HSD ($p < 0.001$). There were no other significant pairwise differences between habitat types.

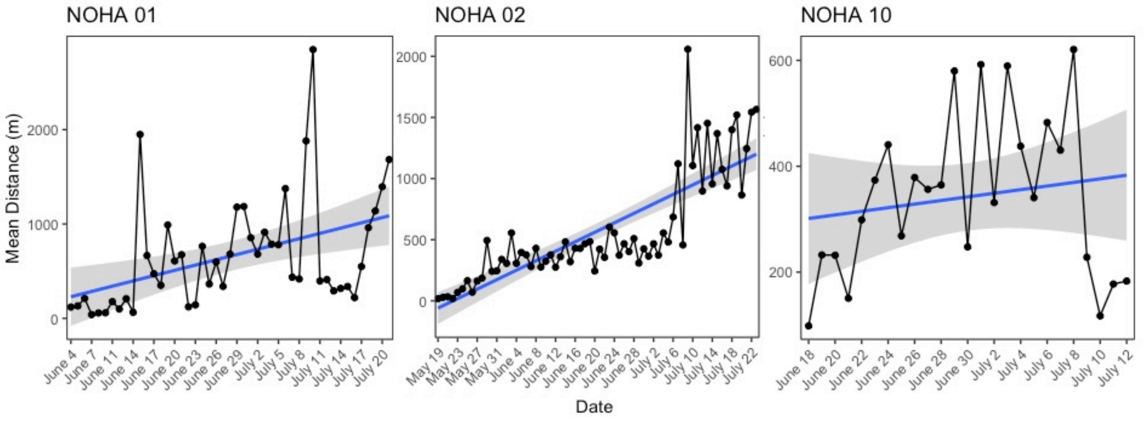

Figure 2.13. Mean distance travelled each day (black line) and the smoothed regression line (blue) with 95% CI (gray shaded area) from the "geom_smooth" function in ggplot2 for three adult breeding female Northern Harriers in Suisun Marsh, CA (2018).

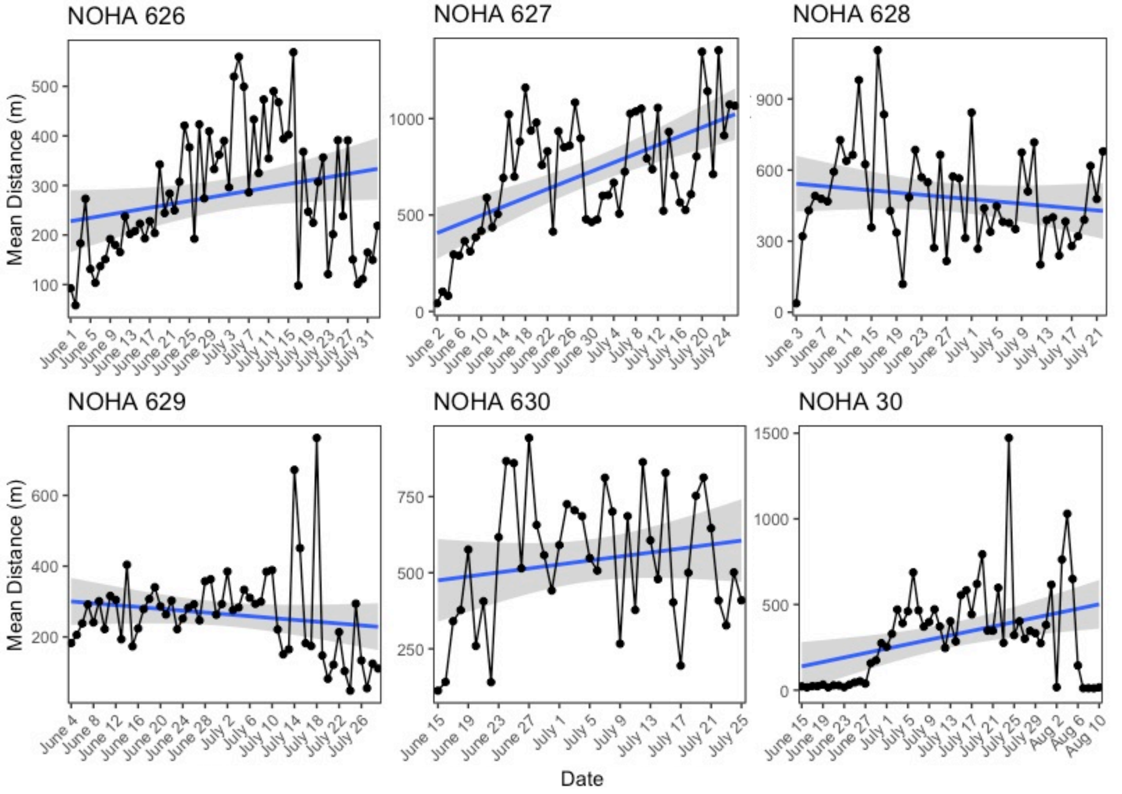

Figure 2.14. Mean distance travelled each day (black line) and the smoothed regression line (blue) with 95% CI (gray shaded area) from the "geom_smooth" function in ggplot2 for six adult breeding female Northern Harriers in Suisun Marsh, CA (2019).

Table 2.10. Mean daily distance traveled (m + sd) to and from the nest site during the nesting period for the first week (seven days) of the nesting period after being marked with a transmitter, the last week (seven days) of the nesting period, and the mean increase in daily distance traveled from the first to the last week of the nesting period for nine adult breeding female Northern Harriers in Suisun Marsh, CA (2018–2019).

	Mean Distance		
ID	**First Week**	**Last Week**	**Mean Increase**
NOHA 01	67.43 (83.94)	1112.17 (1115.60)	1044.74
NOHA 02	67.20 (105.00)	1296.85 (1684.66)	1299.64
NOHA 10	265.82 (261.58)	321.17 (462.58)	55.34
NOHA 626	139.81 (161.25)	183.85 (317.32)	44.04
NOHA 627	212.49 (267.63)	1085.33 (1116.85)	872.84
NOHA 628	415.60 (645.82)	440.54 (625.47)	24.94
NOHA 629	240.38 (260.48)	128.81 (205.84)	-111.57
NOHA 630	309.82 (449.78)	541.40 (785.59)	231.58
NOHA 30	23.09 (39.47)	142.70 (396.39)	119.62
Mean	*193.52 (252.77)*	*583.65 (745.59)*	*390.13*

4. Discussion

Our results reveal differences in habitat selection at three spatial scales (microhabitat, macrohabitat, and home range) that have important management implications for breeding Northern Harriers in Suisun Marsh. At the microhabitat scale, harriers are more likely to select tall vegetation consisting of emergent wetland plants or terrestrial grasses, and California rose. This is consistent with selection for vegetation structure that serves to conceal and protect nests from predators may be more important than vegetation species or habitat type. At the macrohabitat scale, harriers show selection for nesting near water and rose, and away from unnestable vegetation, with a strong selection against nesting near ATV tracks on GIWA, which could represent a sensitivity to disturbance. Harriers also show a strong selection for proximity to other harrier nests, at least on GIWA, highlighting the importance of colonial nesting in our population. Overall, 75% of nests were found in marsh habitat (managed and tidal) compared to upland habitat, and nest densities were very low, suggesting not only a reduction in the harrier breeding population, but also a potential shift in habitat selection from upland habitat to marsh habitat over the past three decades (Loughman and McLandress 1994). Female harrier home ranges are largely within open marsh and grassland habitat types, close to water, and away from shrubland, complementing our macrohabitat selection results. Female home ranges were relatively small, but increased in size across the breeding season, with increased average distance traveled at the end of the breeding season suggesting female foraging forays became more frequent and farther from the nest as nestlings got older. Nestling energy demands decrease after the first two weeks, so it is more likely that females forage farther from the nest as a result of either depleted prey near the nest, or to search for larger prey items to meet the energy needs of both the nestlings and the adult female (Brodin et al. 2003). Despite the importance of voles to breeding harrier populations elsewhere (Hamerstrom 1979, Hamerstrom et al. 1985, Simmons et al. 1986b), vole populations were extremely low across all three years of our study. Further, other small mammal populations did not predict nest site selection, despite following seemingly similar population trends of voles each year.

Average height and density (visual obstruction) of vegetation at the nest in our study was consistent with results from other studies where harriers selected average vegetation anywhere from 57–106-cm tall with an average visual obstruction of 38–49 cm (Toland 1986, Christansen and Reinert 1990, Kantrud and Higgins 1992, Dechant et al. 1998, Evrard and Bacon 1998). Probability of selection was greatest at vegetation 80–100 cm tall in our study, and though visual obstruction (i.e., vegetation density) was not a strong predictor of nest site selection, visual obstruction was 16.6 cm (± 5.08 cm) taller, on average, than at random sites. Interestingly, average live vegetation height at harrier nests in Suisun from 1987–1992 was only 47 cm (Loughman and McLandress 1994) versus 103 cm in our study, though nests 30 years ago occurred primarily in upland habitat dominated by terrestrial annual grasses, compared to marsh habitat dominated by emergent perennial vegetation in our study, though our study included tidal nests which were not monitored from 1987–1992.

The selection of nest sites with almost all or little terrestrial grasses may represent a selection for either marsh or upland habitat in our population. Harrier nests were three times more likely to be found in marsh habitat (managed and tidal combined) than in upland fields. Upland habitat represents approximately 30% (113 km^2) of the available nesting habitat in Suisun, with nearly 60% (210 km^2) represented by managed marsh. However, tidal marsh habitat represents only 10% (32 km^2) of available nesting habitat, yet slightly more nests were found in tidal marsh than upland habitat, suggesting a possible selection for tidal marsh or at least emergent vegetation. This is further supported by the fact that proportion of terrestrial vegetation was not a predictor in the top model for nests on GIWA where no tidal marsh is present and 66% of nests were found in managed marsh, despite nearly half of the wildlife area representing upland habitat (16 of 36 km^2; Ackerman 2002). Selection for emergent wetland vegetation has been found to be variable across populations, with some showing strong selection for cattail (*Typha*), bulrushes (*Scirpus, Schoenoplectus*), sedges (*Carex*), and Common Reed (*Phragmites*), while others strongly selected undisturbed grasslands with various annual grasses and forbs (Dechant et al. 1998). Further, despite several harrier nests occurring in Common Reed in our study there was no clear selection for this species at the nest or proximity to nests on the landscape. Regardless, more research is needed to determine if Common Reed removal efforts will be detrimental to harrier nesting. With the Suisun Marsh Habitat Management, Restoration, and Preservation Plan's (2013) goal of restoring 20–28 km^2 of additional tidal marsh habitat, as well as improving 160–200 km^2 of managed marshes, this could significantly increase preferred nesting habitat availability for harriers. It is important to note, however, that selection of habitat type was not supported by model selection, and the nest site selection may be more related to vegetation structure (Dechant et al. 1998), nest density (Toland 1985, Messmer 1990, Sedivec 1994), social structure (i.e., the prevalence of polygyny in the population; Simmons and Smith 1985, Simmons et al. 1986a), prey population (Hamerstrom 1979), field size (Toland 1986, Murphy 1993), habitat management (Duebbert and Lokemoen 1977, Herkert et al. 1999, Vukovich 2000, Vukovich and Ritchison 2006), or even field moisture (Simmons and Smith 1985), among other factors, regardless of habitat type. We explore some of these factors below.

The probability of nest site selection with some California Rose suggests the selection of vegetation structure that provides nest defense from terrestrial predators. In other populations, harriers selected nest sites in rose (Sealy 1967, Apfelbaum and Seelbach 1983, Christansen and Reinert 1990), blackberry brambles (Apfelbaum and Seelbach 1983, Toland 1985, 1986), or raspberry (Hamerstrom and Kopeny 1981), but the frequency of selection varied significantly across studies from as few as one nest to as many as all nests despite abundant suitable terrestrial grasses. If nest sites in thorny vegetation have high nest survival, the argument for selecting thorny vegetation for nest defense could be made stronger (Toland 1986). Anecdotally, we found that nests in rose were more challenging to access and had fewer failures due to predation.

At the macrohabitat scale, harriers had a higher probability of selecting nest sites at a close distance from water (~100 m) in Suisun and on GIWA. In fact, in 2017 there was record precipitation the winter prior to the breeding season that resulted in excessive flooding across Suisun (the second-highest year since records began in 1895, https://www.mercurynews.com /2017/04/06/california-storms-this-water-year-now-ranks-2nd-all-time-in-122-years-of-records/). Despite this, harrier nests were only ~14 m closer to water in 2017 than in 2018 and 2019, on average, suggesting a clear selection to nest at an optimal distance from water even with excessive water on the landscape. Additionally, the probability of selecting nest sites near water was considerably closer than other distance to landscape variables measured. Simmons and Smith (1985) found that harriers selected wet sites for their nests (where there was either standing water or saturated ground beneath the nest) and that moisture at the nest was a significant predictor of nest success. Nesting near water has been observed in other harrier populations, as well (Sealy 1967, Grant et al. 1991), and has been described as an adaptive trait for predator avoidance in harriers (Sealy 1967, Simmons and Smith 1985), and various waterbird and passerine species (e.g., Burger 1974, Picman et al. 1993, Cain et al. 2003, Hoover 2006). In our study, tidal marsh nests regularly had water below nests and few predation events occurred (unpublished data). Additionally, Montevecchi (1978) argued that nests in dense vegetation in tidal marshes were less likely to be destroyed during high tide events, and that the tallest, most dense vegetation occurred closer to the water's edge. Further, continued nest building throughout the breeding season exhibited by many water birds, as well as harriers, and plasticity in nest height in tidal systems could be adaptive solutions to prevent nest failures due to flooding (Burger 1974, Robertson and Olsen 2015, Clauser and McRae 2016). The selection for nest sites near water, therefore, may represent a trade-off between risk of flooding and protection from predation.

The strong avoidance of shrub habitat (unnestable vegetation) in our population is consistent with our observations, but conflicts with habitat selection in other populations, which have shown strong selection for shrubs at nest sites (Dechant et al. 1998). Shrubs can certainly provide structural cover, but selection of shrubs may be maladaptive in systems with high mesopredator populations, like Coyotes (*Canis latrans*) and Raccoons (*Procyon lotor*), that are attracted to shrubs for cover and may encounter ground nests in or near shrubs (Cooper et al. 2015). That the probability of selection decreases after 2 km from unnestable vegetation in our study is more likely a result of the spatial distribution of unnestable vegetation across Suisun than an actual selection for an optimal distance away since shrub species are found throughout Suisun and there are few areas where no shrubs occur at all. On GIWA, however, harriers had a higher probability of nest sites close to rose and farther away from quail bush (a shrub species included in the unnestable vegetation variable), though these responses were both represented by convex quadratic functions, suggesting either a difference in selection by some harriers (i.e., some prefer to be near rose or quail bush while others do not), or a function of the spatial distribution of these species on the landscape, as described above. It is more likely that the probability of nest sites near or in rose reflects selection of rose as a nest substrate since some nests were found in rose bushes and the proportion of rose at the microhabitat scale was a predictor of nest site selection. By contrast, the selection near or in quail bush more likely reflects the spatial distribution of quail bush across the landscape since no harrier nests were found in quail bush in our study.

Nests found on GIWA differed in macrohabitat selection from Suisun-wide nests in two important ways: harriers exhibited a strong selection for nest sites near other harrier nests in the competition model and an avoidance of ATV tracks in the landscape features model. Harriers have been described as semicolonial nesters in other studies (Hamerstrom 1969, Simmons and Smith 1985). Semicolonial nesting is hypothesized to have evolved for nest defense from corvids and terrestrial mammalian predators, and typically results in increased nest success (Kitowski 2008, Krupiński et al. 2010). However, Simmons (1983) observed little group defense against predators in Northern Harrier colonies. This result could reflect a high prevalence of nest predators at our study site compared to other sites. Alternatively, semicolonial nesting may be an indicator of good habitat quality and could help managers determine the best breeding locations to focus habitat management and protection efforts. In our study, colonies occurred in the same general locations each year.

The avoidance of ATV tracks was strong in the landscape features model and could represent an avoidance of human disturbance and/or reduced habitat quality. Waterfowl nest searching began as early as late March each year on GIWA and continued throughout the breeding season. Individual fields were searched for new nests every three weeks, but previously found waterfowl nests were visited every week for a variety of research activities (Croston et al. 2018, 2021; McDuie et al. 2019, Peterson et al. 2019, Casazza et al. 2020). Though efforts were made to reduce disturbance by following nest check schedules, because of the abundance of different research activities taking place, ATVs were regularly in fields and disturbance to nesting birds undoubtedly occurred (e.g., birds were accidentally flushed from nests, or waterfowl nests near harrier nests had to be visited). Additionally, consistent ATV tracks were used each year to minimize disturbance to vegetation throughout each field, but this inevitably led to visible tracks of trampled vegetation that could have reduced habitat quality or increased mammalian predation by creating corridors throughout fields (Ackerman 2002). Indeed, the use of linear corridors, like levees and roads, by mesopredators of waterfowl nests has been found to significantly increase nest predation and failure (Frey and Conover 2006). Balancing the needs of multiple research activities with disturbance to ground-nesting species must be carefully considered, especially when working near sensitive or listed species.

At the home range scale adult females selected wetland habitat significantly more than any other habitat types, followed by grassland habitat as the second most frequently used habitat type. Though most nest sites were in managed marshes, which were classified as wetland habitat in the landcover map, the use of grassland habitat may represent a partition of habitat types for foraging. Focal observations of individuals coupled with GPS transmitter locations could reveal behavioral differences between these two habitat types. Habitat use within female home ranges also highlights two important findings: female home ranges remained within Suisun boundaries, and females did not select pasture or agricultural habitats surrounding Suisun as foraging areas. Harriers are known to forage in suitable agriculture, like alfalfa, which is common outside of Suisun, but may either be too far away, or may be hunted more frequently by males (Martin 1987). Further, it is not until nestlings are at least 2 weeks old that females begin to forage in addition to males (Martin 1987). This was confirmed by our finding that females made farther foraging forays from the nest as nestlings got older. Male harriers are known to have significantly larger home range sizes than females and travel much farther distances from nest sites to foraging areas (Craighead and Craighead 1956, Barnard 1983, Thompson-Hanson 1984, Toland 1985, Martin 1987), indicating that prey abundance in foraging areas and habitat characteristics at nest sites may be two separate factors influencing nest site selection. Further, males are known to provide all prey to incubating and brooding females early in the breeding season (Martin 1987, Smith et al. 2020), and most of the prey items males deliver are small relative to females that tend to bring larger prey items to the nest as nestlings get older (Bildstein

1987, and unpublished data), though males do exhibit prey switching (from small mammals to birds) across the breeding season as local prey populations fluctuate (Martin 1987). These observations support the hypothesis that there is habitat and resource partitioning between males and females leading to different nest site selection criteria. Future studies aimed at understanding male harrier habitat selection and foraging during the incubation and early brood-rearing stages using GPS transmitters only recently made small enough for males could help elucidate these differences.

We did not find small mammal abundance in the spring to affect nest site selection either by analyzing individual species (harvest mice and house mice) or all small mammals combined at the 1 km^2 or 5 km^2 female home range sizes. Unlike Short-eared Owls (*Asio flammeus*), which are known to select nest sites based on local vole abundance (e.g., Village 1987), male harriers may select territories near suitable foraging areas (but outside primary nest sites). By contrast, female harriers select specific nest sites within territories based on habitat characteristics regardless of local prey populations since males provide all prey to females during incubation and up to the third week after eggs hatch (Martin 1987). Voles are known to influence metrics of harrier reproduction and success in other populations (Hamerstrom 1979, Hamerstrom et al. 1985, Simmons et al. 1986b), but vole abundance in our study was very low, with only five voles captured as the highest number in 2018. As such, we were not able to calculate vole-specific abundance in this study. Vole abundance also significantly influences waterfowl nest success in Suisun by providing consistent and alternative prey to predators (Ackerman 2002), and waterfowl nest predators have changed over the past three decades, suggesting a shift in available alternative prey resources, like voles (Croston et al. 2018). Further, the breeding waterfowl population in Suisun has also declined in recent decades (Feldheim et al. 2018). Taken together the reduced vole densities in Suisun could be an indicator of ecosystem health reflected in lower harrier and waterfowl breeding densities, as well, though more research is needed to determine if this relationship occurs in Suisun.

Management of upland fields and managed marshes differs drastically in Suisun and could have major effects on the factors listed above. Upland fields are typically partially mowed each year with no seasonal flooding and are primarily managed for breeding waterfowl and upland game bird hunting. Managed marshes are largely undisturbed (i.e., little to no mowing) but with seasonal controlled flooding for wintering waterfowl. Tidal marshes, however, are completely unmanaged and undisturbed, and are subject to natural tidal inundation with mostly native emergent plant species and a dense thatch layer providing an elevated nesting substrate above tidally influenced water levels. Harriers in other populations have strong selection for undisturbed grassland (i.e., not mowed, grazed, or burned for > 1 year, but up to 3 to 5 years) and wetland habitat (Duebbert and Lokemoen 1977, Apfelbaum and Seelbach 1983, Toland 1985, 1986; Kantrud and Higgins 1992, Dechant et al. 1998). Small mammal populations also respond positively to undisturbed habitats (Slade and Crain 2006), with one study finding vole populations to be twice as high in undisturbed habitats than highly disturbed habitats, like agricultural fields (Koks et al. 2007). Harriers in our population may be selecting undisturbed habitats for both superior habitat quality and higher local small mammal populations.

Lastly, the average harrier nesting density from 1987–1992 was 8.4 nests km^{2-1} (range: 3.3 to 24.8 nests km^{2-1}) on GIWA with nests occurring almost exclusively in upland habitat (Loughman and McLandress 1994). By comparison, average nest density was 0.42 nests km^{2-1} and 0.44 nests km^{2-1} across Suisun and on GIWA, respectively, across all three years of our study. Even if we restrict nest density calculations to nests that occurred in the upland habitat on

GIWA (8 km^2) to be comparable to densities calculated by Loughman and McLandress (1994), average nest density in our study was only 0.59 nests km^{2-1} (range: 0.38 to 0.88 nests km^{2-1}), with a total of only 14 nests occurring in upland fields across all three years (4.7 nests/year on average) compared to 150 nests from 1987–1992 (25 nests/year on average). This represents a nearly 14.5-fold decrease in nesting densities over the past three decades. Harrier nesting densities have clearly significantly decreased across Suisun, but whether there has also been a shift from upland habitat to marsh habitat and whether changes to habitat management or disturbance have influenced this shift are still unknown.

5. Management Implications

Habitat management considering spatial scale could greatly influence nest site selection and improve nesting habitat for harriers in Suisun. At the microhabitat scale, managers should focus on providing tall, dense, emergent wetland vegetation that provides both structure and cover. Upland habitat may provide more suitable nesting habitat for harriers once again if management efforts focus on increasing small mammal populations, especially voles, and reducing disturbance (i.e., limit mowing or research activities). California Rose, specifically, may provide important vegetation structure to deter mammalian predators, which are the primary nest predators. At the macrohabitat scale, maintaining a balance between suitable dry habitat for nest placement, but with relatively close wet areas could reduce mammalian predation, as well. Further, managing habitat for large patches of open habitat that support nesting colonies is also important for harriers, and identifying colonies each year can help managers reduce disturbance and protect habitat in these areas.

Shrub and tree management may also be important in Suisun. Shrub and tree encroachment on open habitats, like wetlands and grasslands, may be detrimental to nest site selection and nest success for harriers and other ground-nesting species alike, and has been found to negatively affect nesting birds in other systems by changing predator communities and predation risks (Davis 2017). Though distance to trees was not a predictor of nest site selection, trees serve as perches and nest sites for raptors and corvids, as well as refugia for mesopredators, like raccoons, skunks, and coyotes. Further, trees often grow along roads and levees, which are already known corridors for predators and could increase predation risks to ground-nesting birds like harriers, waterfowl, waterbirds, gamebirds, and grassland-nesting passerines in Suisun. Staggering management efforts, like mowing or burning, to reduce shrub encroachment (Zuckerberg and Vickery 2006), while maintaining large areas with completely undisturbed habitat (at least > 1 year) may help restore suitable nesting habitat and improve harrier and other ground-nesting bird reproduction.

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trapping was conducted under a USFWS section 10(a)(1)(A) recovery permit #TE-020548-14, a CDFW Scientific Collection Permit #SC-005749, a Memorandum of Understanding (MOU) between USGS and CDFW, and IACUC protocol #19806. Use of trade, product or firm names does not imply endorsement by the U.S. Government.

Chapter 3: The importance of habitat and prey on Northern Harrier (*Circus hudsonius*) nest success in Suisun Marsh, California

Abstract

Breeding populations of Northern Harriers (hereafter "harriers", *Circus hudsonius*) have been in decline across their range, primarily due to habitat loss. Harriers select tall vegetation for nest sites in marsh and grassland habitats, both of which primarily occur on protected state and federal lands across California. Understanding how nest habitat and other factors at different spatial scales influence nest survival will allow habitat managers to improve habitat and maximize reproductive success. We studied how factors related to nest timing, microhabitat, macrohabitat, prey densities, and habitat types affect nest survival using logistic exposure models for harriers breeding in Suisun Marsh, California. We found apparent nest success to be relatively low (40%) compared to nest survival in populations across their range, but Mayfield's survival to be similar to that of harrier nests in Suisun Marsh three decades ago. Despite similar survival rates, the number of nests and nest density has significantly declined over the past three decades, revealing a declining population with already low nest success. Higher spring small mammal densities had a positive effect on nest survival, and high summer small mammal density positively influenced the number of fledglings. However, California Voles (*Microtus californicus*), an important prey item for harriers, are alarmingly low in Suisun Marsh compared to historical observations. Improving vole populations could improve harrier nest survival and increase the breeding population in Suisun Marsh. Our results also suggest that a high proportion of live vegetation and residual vegetation present at the nest are important microhabitat characteristics that influence nest survival. Further, nests closer to California Rose (*Rosa*

californicus) also have higher nest survival, which is consistent with nest site selection determined in Chapter 2. Lastly, nest survival is highest in managed marsh habitat, despite potential selection for tidal marsh habitat, as well. Lower nest survival in tidal marsh habitat may be influenced by inappropriate habitat structure and extreme flooding events that could be exacerbated by sea level rise in the future. Restoring tidal marsh to large, contiguous habitat patches with numerous smaller channels to better diffuse the effects of high tides across the tidal plane could reduce nest flooding for harriers and other sensitive tidal marsh species in Suisun Marsh.

1. Introduction

Northern Harriers (*Circus hudsonius*; hereafter "harriers") are a widespread North American raptor species found primarily in wetland and grassland ecosystems, as well as relatively undisturbed agriculture and pasture habitats (Smith et al. 2020). Harrier breeding populations are undergoing local declines across their range, primarily due to habitat loss (Smith et al. 2020). Harriers have no federal listing status under the U.S. Endangered Species Act, but they are listed as endangered, threatened, or sensitive in several states. In California, harriers are listed as a Species of Special Concern (Shuford and Gardali 2008), which highlights the need for research to better understand harrier declines across the state. Suisun Marsh (hereafter "Suisun") part of the San Francisco Bay-Delta Estuary has one of the largest breeding populations of harriers in California, though number of nests and breeding densities have significantly declined over the past three decades (See Chapter 2, Loughman and McLandress 1994, Shuford and Gardali 2008). With the breeding population reduced, it is important to determine if nest success has also declined and what factors may have caused this decline. Suisun is a unique breeding site compared to other harrier breeding sites across their range. The use of tidal marsh habitat in addition to managed marsh and grassland habitats for nesting harriers (Chapter 2) could affect the selection and success of nest sites due to differential vegetation composition and tidal influences. For example, sea level rise and extreme flooding events due to climate change have already been documented (e.g., Ma et al. 2019) or predicted (Reynolds et al. 2015) as threats to tidal-nesting birds. If harriers select tidal marsh habitat but suffer reduced nest success as a result of climate change induced extreme flooding events, tidal marsh could become an ecological trap.

Despite their population declines and loss of habitat, as far as we know there has only been one incidental study (Loughman and McLandress 1994), and one targeted harrier study (Thompson-Hanson 1984) reporting nest success in the Western United States. All other targeted studies are almost exclusively from the Great Plains region of the United States and Canada (Saunders 1913, Breckenridge 1935, Hammond and Henry 1949, Craighead and Craighead 1956, Sealy 1967, Hamerstrom 1969, 1979; Follen Sr. 1975, Duebbert and Lokemoen 1977, Apfelbaum and Seelbach 1983, Hamerstrom et al. 1985, Toland 1985, 1986; Evrard and Bacon 1998, Vukovich and Ritchison 2006, Datta 2016). Only a handful of studies have been conducted in the Northeast (Dunne 1984, Simmons and Smith 1985, Simmons et al. 1986b, a; Barnard et al. 1987, Serrentino 1987, Simmons 1988), and even fewer have reported harriers nesting in tidal marsh habitat (Tate and Melvin n.d., Holt and Melvin 1986). Further, many of these studies simply report reproductive metrics (apparent nest success, number of nests, clutch sizes, etc.) without studying the factors that influence nest success. There have been no targeted studies of nesting harriers in California outside of the current study, with all harrier monitoring to date focusing on the effects of harrier predation on nesting shorebirds and other sensitive tidal species

(Evens and Page 1986, Donehower and Tokatlian 2012, Frost 2015, Casazza et al. 2016, Thorne et al. 2019).

Harriers breed in tall, dense vegetation typically dominated by either wetland emergent plants or terrestrial grasses across their range (Chapter 2, Smith et al. 2020). Though the general nest vegetation structure is relatively consistent across populations, individual populations select different and sometimes very specific species of vegetation for nest sites that could have varying local impacts on nest success and habitat management practices. For example, harriers breeding in southwest Missouri nested exclusively (during 1984) or nearly exclusively (93% in 1985) in blackberry brambles (*Rubus* sp.) despite abundant available suitable grassland vegetation (Toland 1985, 1986), whereas harriers breeding in Wisconsin primarily placed nests in terrestrial and emergent grasses and forbs, with less than five nests (*n* = 184) found in raspberry brambles (*Rubus* sp., Hamerstrom and Kopeny 1981). These contrasting nest site selections indicate the need for population-specific habitat management plans that meet the needs of each population and ensure the highest nest success possible.

Nest timing events, like nest initiation, days since the first egg was laid, and when nests were observed may also play important roles in nest success. The more recent development and increasing popularity of the logistic-exposure method (Shaffer 2004) over the traditional Mayfield method (Mayfield 1961, 1975) of estimating nest survival has the advantage of accounting for this variability and revealing finer-scale changes in nest survival throughout the nesting season (e.g., Grant et al. 2005, Lloyd and Tewksbury 2007, Crimmins et al. 2016). In many passerines, nest survival is high at nest initiation and declines throughout the season (Grant et al. 2005), but in some species declines in nest survival during specific periods of the nesting season (e.g., hatching) occur and can reveal sensitive periods in the nesting season. For example, Crimmins and colleagues (2016) found that daily nest survival for Henlow's Sparrows (*Ammodramus henslowii*) was lowest at the onset of hatching and increases to pre-hatch rates thereafter. This information can help managers develop strategies specific to protecting nests during this sensitive period. In harriers in New Brunswick, Canada a similar trend has been observed where nest success overall declines throughout the season, but nests that are initiated early tend to have higher success than nests initiated later (Barnard et al. 1987).

Early initiated nests may have higher nest success for a variety of reasons. In a polygynous mating system, like in harriers, early initiated nests often belong to primary females, which receive the most provisioning from males and have higher nest success than secondary females (Hamerstrom et al. 1985, Simmons et al. 1986b, a; Simmons 1988). However, harriers initiating nests early may also be employing an adaptive strategy to match hatch timing of their own young with hatch timing of available passerine prey species (Barnard et al. 1987) or population peaks in preferred small mammal species like voles (Simmons et al. 1986b). This idea is strengthened by the fact that nest success is highly correlated to prey abundance in several populations (Hamerstrom 1979, Hamerstrom et al. 1985, Simmons et al. 1986b, Barnard et al. 1987). Phenological shifts in migration and nest timing are becoming more widespread with ongoing climate change (Jones and Cresswell 2010, van Buskirk 2012, Jaffré et al. 2013). If specialist predator species do not shift nest timing appropriately, they may be affected by phenological mismatches that could drastically influence nest success (Durant et al. 2007).

In Suisun, harriers select vegetation at the nest, approximately 1-m tall with much California Rose (*Rosa californicus*). They also select both high and low proportions of terrestrial grasses, indicating a potential selection for two different habitat types, tidal and managed marsh and upland fields. Harriers select nest sites ~ 100 m from water and > 2000 m from woody shrub vegetation, both of which may be responses to predation (Chapter 2, Simmons and Smith 1985, Vukovich and Ritchison 2006). On the Grizzly Island Wildlife Area (GIWA) within Suisun, where extensive wildlife research occurs, harriers select nest sites away from all-terrain vehicle (ATV) tracks that may indicate an avoidance of human disturbance and predators that use ATV tracks as movement corridors through nesting habitat (Chapter 2). Harriers on GIWA also show strong semicolonial nest site selection, which may be indicative of their polygynous mating system, local vole populations, and/or habitat quality (Chapter 2, Simmons and Smith 1985). Connecting habitat selection, prey populations, and breeding behavior to nest success is an important step towards improving harrier conservation and management in Suisun Marsh.

In this study we investigated factors influencing nest success that are related to 1) nest timing events, 2) microhabitat (nest-level), 3) macrohabitat (landscape-level), 4) prey density, and 5) habitat types. We hypothesize that nest initiation will affect nest survival, with early-initiated nests having higher survival than late-initiated nests. We also hypothesize that higher spring small mammal densities would influence measures of reproductive success, like number of nests, clutch sizes, and number of nestlings. Given the results from our nest-site selection research (Chapter 2), we hypothesize that nests with more California Rose (*R. californicus*) would prevent predation and have higher nest survival. Nests in managed marsh should also have higher survival because nests in other habitat types will either be too wet (tidal marsh) or too dry and/or disturbed (upland habitat), leading to increased nest failure due to flooding, disturbance, or predation. Lastly, we hypothesized that high summer small mammal densities near the end of the breeding season will increase the number of fledglings and nest survival.

2. Methods

2.1 Study Area

This study was conducted in Suisun Marsh, CA on the Grizzly Island Wildlife Area (GIWA) and surrounding private duck hunting clubs and properties owned by non-profit organizations (38.1515° N, 121.9717° W; see detailed description in Chapter 2, Fig 2.1 Chapter 2).

2.2 Nest Visits

Detailed nest survey and access methodology has been described in Chapter 2. At each initial nest visit we recorded the number of eggs and/or nestlings, color of eggs, and GPS location. We promptly left if no nestlings were present to minimize disturbance to the incubating female. If only eggs were present, the number and color of eggs were used to determine approximate hatch dates. If there were only 1-3 eggs, typically the clutch was incomplete. If there were 4-6 eggs, typically the clutch was complete (Macwhirter and Bildstein 1996). When harrier eggs are first laid, the light blue shell membrane is visible through the eggshell for the first ~ 48 hrs, giving it a blue color (Hamerstrom 1969, Scharf and Hamerstrom 1975), turning white after this period (Fig. 3.1). If any eggs were blue, we could determine approximate laying date, back calculate when any other white eggs present were laid (based on a 2-day laying interval; Smith et al. 2020), and then add 30 d (average incubation length; Smith et al. 2020) to the date of the first egg laid for an approximate hatch date. If we were able to estimate a hatch date, we visited the nest again on this date. If no eggs were blue and the clutch was incomplete, we next visited the nest in three weeks. If no eggs were blue and the clutch was complete, we visited the nest in two weeks. These visit schedules allowed for minimization of disturbance to incubating females while allowing us to capture hatching as early as possible.

If nestlings were present at the initial nest visit, we recorded the following characteristics: nestling/egg age, estimated based on size and the number of nestlings and eggs present based on a two-day hatching interval; eye color; sex, based on eye color, which diverge beginning at ~ 9–11 days of age with brown eyes = female, and gray = male (Hamerstrom 1968; personal observation; weight; wing chord; length of the sixth primary (the longest primary in nestlings, measured between the fifth and sixth primaries; Scharf and Balfour 1971); tail length; egg tooth characteristics (present or absent); talon color (clear, gray, black); and, crop characteristics (full, partial, empty). Nestlings were marked with either a unique nail polish color on the talons of one foot, and/or a unique number of small non-toxic paint dots on the back of their head for individual recognition at repeat visits. Nestling measurements repeated every 4-5 days in 2017 and every 3-4 days in 2018 and 2019. Before fledging, nestlings were banded with a USGS aluminum lock-on leg band. Nests were considered successful if at least one nestling fledged. We attempted to determine the reason for all failed nests, including predation, flooding, abandonment (natural or research-induced), or unknown.

After each nest visit, we watched the adult female return to the nest from 100-500 m away with binoculars and recorded the amount of time it took for her to return for up to 30 mins from the incubation stage to approximately two weeks of age for the youngest nestling, after which females do not regularly brood nestlings nor return quickly. This was recorded to determine if researcher nest disturbance affected nest abandonment in the late incubation or early brooding stages.

Figure 3.1. Three harrier nests with examples of both blue and white eggs used to estimate approximate hatch dates. (A) One blue egg on the top left with the remaining four eggs white, (B) two blue eggs on the top with one white egg at the bottom, and (C) one blue egg on the top left with the remaining four eggs white. Photo credit: Shannon Skalos.

2.3 Small Mammal Trapping and Density Estimates

Small mammal trapping methodology has been described in detail in Chapter 2. In addition to spring trapping (Chapter 2), we also trapped small mammals in the summer across all three years of this study (2017–2019) to estimate density and abundance at the end of the harrier breeding season. We randomly sampled the same pairs of grids sampled in the Spring across all four habitat types (managed marsh, upland fields, tidal marsh, and pasture).

Density and abundance estimates were calculated using the same methodology described in Chapter 2, using open spatial recapture models (“oSCR” package) and a normalized difference vegetation index (NDVI) raster for July of each year as the predictor variable. We calculated density and abundance estimates for each small mammal species captured, as well as all small mammals combined. All analyses were performed in Program R (version 3.6.3; R Core Team 2020).

2.4 Nest Timing and Nest Metrics

We used logistic-exposure models to investigate the effects of nest timing variables on nest survival for all nests, including initiation date (date first egg was laid), nest age (days since first egg was laid), and observation age (days since nest was first found) (Shaffer 2004, Bolker 2019). The logistic-exposure models utilized a modified logit link function to account for variation in time between nest visits (Shaffer 2004, Crimmins et al. 2016). Additionally, we tested whether nests that were initiated and hatched during the early vs. the late period of the nesting season differed in nest survival by splitting the data by the median date for each timing event. We used the same model selection approach detailed in Chapter 2. Any predictors with a Pearson's r coefficient of > |0.65| or VIF > 4 were considered collinear and were restricted from occurring in the same model together during model selection (Dyson et al. 2019). We specified nest ID as a random effect in all models and we assessed model fit by visualizing the receiver operating characteristic curve (ROC) and calculating area under the curve (AUC) for all top models. We also used Poisson regression models to test the effects of spring and summer small mammal density at scales of 1 km^2 (adult female home range) and 5 km^2 (adult male home range) on clutch size, number of nestlings, number of fledglings, and number of nests. Finally, we calculated apparent nest success (number of nests that fledged at least one nestling/total number of nests), as well as daily survival probability and overall nest survival probability using the Mayfield (1975) method to be comparable to other published studies. We used the difference between the median fledge day and the median initiation day as the total nesting season length

(69 d, see results). Overall nest survival probabilities were calculated by raising the daily survival probability (for both Mayfield- and logistic-exposure-derived probabilities) by the total nesting season length (e.g., 0.99 daily survival probability$^{\wedge 69\ \text{d nesting season}}$ = 0.50 nest survival probability). All analyses were performed in Program R (version 3.6.3; R Core Team 2020).

2.5 Microhabitat Nest Success

Microhabitat nest site measurement methodology has been described in detail in Chapter 2. We used logistic-exposure models to estimate nest survival probability (Shaffer 2004, Bolker 2019) using the suite of nest site habitat characteristics as predictor variables (Table 2.1, Chapter 2) and the same two-stage modeling approach described in Chapter 2. We repeated these analyses for all nests across Suisun, as well as the subset of nests that occur on GIWA only. All analyses were performed in Program R (version 3.6.3; R Core Team 2020).

2.6 Macrohabitat Nest Success

Macrohabitat nest site measurement methodology has been described in detail in Chapter 2. We used logistic-exposure models described above in a three-stage modeling approach described in detail in Chapter 2 for all nests across Suisun, as well as the subset of nests that occur on GIWA only. We also included ATV tracks in the landscape features model class, as well as a competition model class, including distance to active raptor or raven stick nests and distance to other harrier nests, similar to Chapter 2. In the third stage (global model), prey density and habitat type were also included in the model combinations, as well as individually. Summary statistics for the variables used in these models can be found in Table 2.7, Chapter 2.

We also performed post-hoc analyses for Suisun and GIWA nests to further investigate the positive relationship between distance to rose and nest survival (see results). We chose micro-and macrohabitat variables that we hypothesized could explain this relationship using simple linear models with linear and quadratic forms of each predictor variable. Predictor variables included average vegetation height and average visual obstruction for all nests on Suisun, plus distance to other harrier nests on GIWA to test if vegetation cover or competition for nest sites increased closer to rose. We followed the same three-stage procedure performed for other analyses. All analyses were performed in Program R (version 3.6.3; R Core Team 2020).

3. Results

3.1 Small Mammal Trapping and Density Estimates

We captured six species of small mammals but report only the three most common species here, which represent 98.7% of all captures (Table 3.1). We captured a total of 1,318 individual small mammals across 1,937 total captures for both spring and summer seasons across all three years (Table 3.1). Harvest mice (Western, *Reithrodontomys megalotis*, and Salt Marsh Harvest Mice, *Reithrodontomys raviventris*, combined) were the most common small mammals captured in total (50.2%), though captures varied from as few as 30 to as many as 355 individuals across seasons and years (Table 3.1). House Mice (*Mus musculus*) were the second most common species captured in total (46.7%) and captures varied from as few as 2 to as many as 562 individuals across seasons and years (Table 3.1). California Voles (*Microtus californicus*) were the third most common species captured, though total captures made up only 1.8% (Table 1). Very few *Rattus* spp. or Deer Mice (*Peromyscus maniculatus*) were captured each year and are not individually reported here though they are included in the total captures for each season and year (Table 3.1). Small mammal populations overall were very low in 2017, high in 2018, and intermediate in 2019, and this pattern was consistent for spring captures each year (Table 3.1). However, summer 2019 had lower captures than summer 2017, and summer 2018 was an intermediate year (Table 3.1).

Density and abundance estimates could not be calculated for voles independently because there were too few captured. Instead, voles were combined with all species and overall density and abundance was estimated for each season and year (Table 3.2). Additionally, we include density and abundance estimates for harvest mice and house mice individually (Table 3.2), though only combined small mammal estimates were included in the nest survival analyses. Each season and year, harvest mice were consistently the most dense and abundant small mammals captured, except during summer 2018 where house mice were the most dense and abundant species (Table 3.2). Overall, small mammal density estimates declined across years for spring seasons, and revealed intermediate-, high-, and low-density years for summer seasons from 2017 to 2019, respectively (Table 3.2).

Table 3.1. Summary of small mammal individual captures (*n*), recaptures, total captures, and proportion (%) of total captures across all spring and summer trapping periods in Suisun Marsh, CA from 2017–2019. Total trap nights for each year were: 3,271 (2017), 4,984 (2018), and 4,975 (2019). Updated 7.8.21 Not shown: *Rattus* sp. and Deer Mouse captures, which equaled < 5 individuals each season–year but these captures are included in the total small mammal data.

Species	**Season**	**Year**	***n***	**Recaptures**	**Total Captures**	**% Captures**
House Mouse	Spring	2017	2	3	5	6.0
		2018	244	78	322	50.6
		2019	35	6	41	20.0
	Summer	2017	55	9	64	38.8
		2018	318	112	430	57.4
		2019	33	10	43	43.4
	Total	2017	57	12	69	27.8
		2018	562	190	752	54.3
		2019	68	16	84	27.6
		Total	687	218	905	46.7
Harvest Mouse[1]	Spring	2017	47	28	75	90.4
		2018	191	105	296	46.5
		2019	106	52	158	77.1
	Summer	2017	50	47	97	58.8
		2018	164	134	298	39.8
		2019	30	19	49	49.5
	Total	2017	97	75	172	69.4
		2018	355	239	594	42.9
		2019	136	71	207	68.1
		Total	588	385	973	50.2
California Vole	Spring	2017	0	0	0	0.0
		2018	5	1	6	0.9
		2019	2	2	4	2.0
	Summer	2017	1	1	2	1.2
		2018	15	3	18	2.4
		2019	5	0	5	5.1
	Total	2017	1	1	2	0.8
		2018	20	4	24	1.7
		2019	7	2	9	3.0
		Total	28	7	35	1.8
	Spring	*2017*	*51*	*32*	*83*	*100*

Total Small Mammals		*2018*	*445*	*191*	*636*	*100*
		2019	*145*	*60*	*205*	*100*
	Summer	*2017*	*108*	*57*	*165*	*100*
		2018	*499*	*250*	*749*	*100*
		2019	*70*	*29*	*99*	*100*
	Total	*2017*	*159*	*89*	*248*	*100*
		2018	*944*	*441*	*1385*	*100*
		2019	*215*	*89*	*304*	*100*
		Total	*1318*	*619*	*1937*	*100*

[1] Includes both Western (*Reithrodontomys megalotis*) and Salt Marsh Harvest Mice (*Reithrodontomys raviventris*).

Table 3.2. Summary statistics from the spatial capture–recapture models fitted to the spring and summer seasons and three years (2017–2019) of small mammal trapping in Suisun Marsh, CA. Species include: House Mouse (*Mus musculus),* Harvest Mouse (Salt Marsh Harvest Mouse, *Reithrodontomys raviventris*, and Western Harvest Mouse, *Reithrodontomys megalotis*, combined), and all small mammals (House Mice, Harvest Mice, Deer Mice, *Peromyscus maniculatus*, Rats, *Rattus* spp., and California Voles, *Microtus californicus*). Estimates are modeled with Normalized Difference Vegetation Index (NDVI) at 250 m grid cell resolution as the predictor variable. Parameter estimates represent mean density (*D*) per 1 km^2, and total abundance (*N*) across the entire state-space including standard error (SE) and 95% confidence interval (CI).

			Density (*D*)			**Abundance (*N*)**		
Species	**Season**	**Year**	**Estimate**	**SE**	**95% CI**	**Estimate**	**SE**	**95% CI**
House Mouse	Spring	2017	14.96	13.50	2.72–98.50	455.97	411.38	82.93–2998.58
		2018	97.74	23.19	61.48–155.83	15287.94	3626.69	9616.97–24374.43
		2019	113.07	55.24	43.90–298.21	6923.12	3382.27	2688.18–18259.12
	Summer	2017	82.56	33.82	37.05–184.61	7859.62	3220.03	3526.69–17575.29
		2018	201.82	22.85	161.47–252.10	35666.20	4038.50	28581.91–44551.82
		2019	39.04	15.99	17.84–89.16	3195.49	1308.48	1460.04–7297.55
Harvest Mouse[1]	Spring	2017	307.69	116.10	148.97–654.12	12504.69	4718.24	6053.96–26583.24
		2018	678.95	100.12	509.34–908.07	98612.89	14541.45	73978.25–131890.03
		2019	94.24	21.96	60.38–150.81	11540.14	2689.66	7394.50–1846.36
	Summer	2017	89.50	24.17	53.73–155.36	6390.63	1726.07	3836.04–11093.01
		2018	156.88	21.06	120.82–204.51	19059.63	2558.67	14678.74–24846.93
		2019	44.37	18.96	20.15–109.46	3622.74	1547.69	1644.65–8936.46
All Small Mammals	Spring	2017	292.94	105.83	145.89–601.47	11904.94	4300.99	5929.08–24443.65
		2018	219.15	27.98	167.03–287.97	36726.43	3995.11	27992.76–48259.99
		2019	148.02	30.45	99.31–224.60	18126.93	5102.4	12162.11–27505.06
	Summer	2017	148.67	27.98	103.13–215.69	21230.04	3995.11	14726.92–30801.09
		2018	264.51	22.09	224.66–311.67	46744.00	3903.42	39702.18–55078.60
		2019	24.68	6.56	14.82–42.07	3462.49	920.44	2078.96–5903.24

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[1] Includes both Western (*Reithrodontomys megalotis*) and Salt Marsh Harvest Mice (*Reithrodontomys raviventris*).

3.2 Nest Timing and Nest Metrics

From 2017–2019 we found and monitored 77 harrier nests in Suisun, 53 of which occurred on Grizzly Island Wildlife Area (GIWA). We found 13 nests in 2017, 30 nests in 2018, and 34 nests in 2019. The average clutch size was 4.3 (range = 1–6, sd = 1.0), the average number of nestlings was 3.6 for nests that hatched at least one egg (range = 1–6, sd = 1.2), and the average number of fledglings was 2.3 for nests that fledged at least one nestling (range = 1–5, sd = 1.1) across all three years.

Apparent nest success was 53.8%, 46.7%, and 29.4% each year, respectively, with an overall apparent nest success rate of 40.3% (31 successful nests). Nest survival probability using the Mayfield method was 5.4%, 25.7%, and 16.3% each year, respectively, with daily survival probabilities of 95.9%, 98.1%, and 97.4% for the three years. Overall nest success using the Mayfield method was 18.2% across all three years with a daily survival probability of 97.6%. Depredation was the primary cause of nest failure (33.8%, 26 nests), followed by nest abandonment (13.0%, 10 nests), and tidal flooding (9.1%, 7 nests). Three nests failed due to unknown causes (3.9%), though two of these nests were suspected to have failed due to tidal flooding. Predator species could not be determined for all depredated nests, but the primary predators based on video monitoring, personal observations, and eggshell remains were Common Raven (*Corvus corax*), Common Raccoon (*Procyon lotor*), and Striped Skunks (*Mephitis mephitis*) during the incubation stage, and Coyote (*Canis latrans*) during the nestling stage. There was one case of a suspected Great Horned Owl (*Bubo virginianus*) injuring a nearly fledged nestling at a successful nest, as well.

The earliest date of initiation across all three years was 28 March (day of year = 87) and the latest date of initiation was 3 June (day of year = 154). Median initiation date was 22 April (day of year = 112, Fig. 3.2). The earliest hatch date across all three years was 27 April (day of year = 117) and the latest hatch date was 3 July (day of year = 184). Median hatch date was 22 May (day of year = 142, Fig. 3.2). The earliest fledge date across all three years was 9 June (day of year = 160) and the latest fledge date was 21 July (day of year = 202). Median fledge date was 30 June (day of year = 181, Fig. 3.2). The earliest fail date across all three years was 18 April (day of year = 109) and latest fail date was 17 July (day of year = 198). Median fail date was 22 May (day of year = 142, Fig. 3.2).

There was no difference in nest survival between early and late initiating ($\beta = 0.04$, 85% CI = -1.00 to 0.85) or hatching nests ($\beta = 0.16$, 85% CI = -0.64 to 1.03) and the null hypothesis was the top model for both analyses. Further, initiation date ($\beta = -0.05$, 85% CI = -0.49 to 0.33), nest age ($\beta = -0.17$, 85% CI = -0.78 to 1.18), and observation age ($\beta = 0.33$, 85% CI = -0.11 to 0.74) did not affect nest survival, with the null hypothesis the top model for all three analyses.

Summer small mammal density at a scale of 1-km^2 was positively correlated with the number of fledglings ($\beta = 1.15$, 85% CI = 0.51–1.80, Fig. 3.3). Neither spring nor summer small mammal density affected the number of nestlings, clutch size, or number of nests across years, with the null hypothesis the top model for all three analyses.

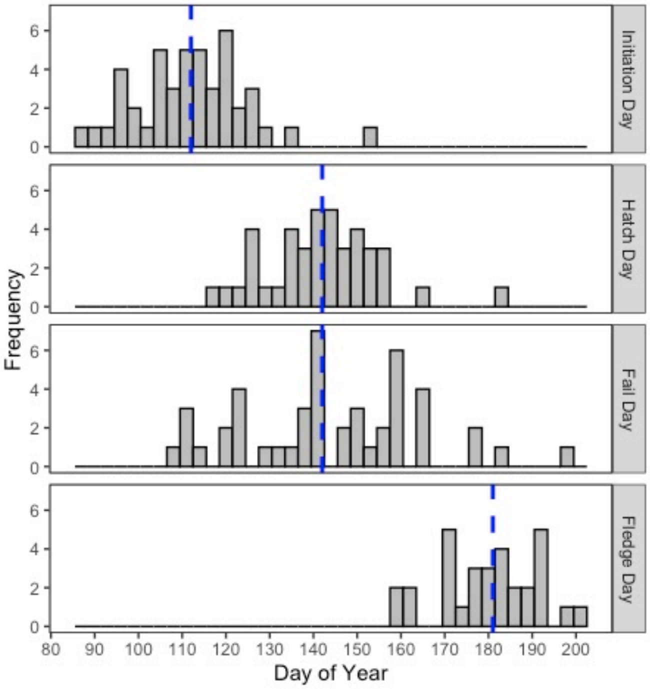

Figure 3.2. Histograms of initiation day, hatch day, fledge day, and fail day with median day of year for each nest timing event (vertical blue dashed line) for Northern Harrier nests in Suisun Marsh, CA (2017–2019).

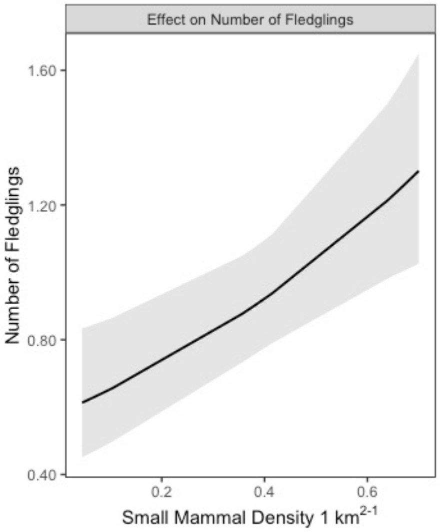

Figure 3.3. Effect of summer small mammal density on Northern Harrier fledglings in Suisun Marsh, CA (2017–2019). Shaded area represents 85% CI.

3.3 Microhabitat Nest Success

Summary statistics of nest site microhabitat characteristics can be found in Table 2.1, Chapter 2. After stage one analyses, only residual vegetation height, proportion live vegetation, and proportion residual vegetation were selected for stage two analysis. The top model that predicted nest survival across Suisun included the quadratic form of residual vegetation height and the linear form of proportion live vegetation at the nest (Table 3.3). Probability of nest survival decreased as residual height increased (β = -0.39, 85% CI = -0.64 to -0.16), and increased with higher proportion of live vegetation at the nest (β = 0.64, 85% CI = 0.33–1.19, Fig. 3.4). The cumulative weights of evidence for residual vegetation height and proportion live vegetation were 0.96 and 0.77, respectively (Table 3.4). Proportion residual vegetation at the nest had a cumulative weight of evidence of 0.21 (Table 3.4) and was not included in the top model.

On GIWA, only residual vegetation height, proportion live vegetation, and proportion terrestrial vegetation were selected for stage two analysis. The top model that predicted nest survival also included the quadratic form of residual vegetation height and the linear form of proportion live vegetation at the nest (Table 3.3). Probability of nest survival was high across a broad range of residual vegetation heights and began to decrease at heights ≥ 100 cm (β = -0.65, % CI = -1.07 to -0.33, Fig. 3.5). Proportion of live vegetation was positively correlated with nest survival (β = 0.94, % CI = 0.47–1.62, Fig. 3.5). The cumulative weights of evidence for residual vegetation height and proportion live vegetation at the nest were 0.95 each (Table 3.4). Proportion terrestrial vegetation at the nest had a cumulative weight of evidence of 0.29 (Table 3.4) and was not included in the top model.

The estimated daily survival rates from the Suisun and GIWA marginal (fixed effects only) global models were 0.92 and 0.99, with overall nest survival probabilities of 0.003 and 0.50, respectively.

Table 3.3. Microhabitat nest survival model sets for harrier nests at different spatial scales in Suisun Marsh, CA from 2017-2019. Model sets represent all competing logistic-exposure models within 2 AIC$_c$ scores of the top model for all model combinations.

Spatial Scale	**Model**	***K***	**–2(*L*)**	**AIC$_c$**	**ΔAIC$_c$**	ω_i
Suisun	% Live + Residual Height^2	3	-95.53	201.23	0.00	0.74
GIWA	% Live + Residual Height^2	3	-44.35	98.97	0.00	0.67

Table 3.4. Cumulative AIC$_c$ weights of evidence ($\sum \omega_i$) of microhabitat nest survival model parameters for harrier nests at different spatial scales in Suisun Marsh, CA from 2017-2019.

Spatial Scale	**Model Parameters**	$\sum \omega_i$
Suisun	Residual Height	0.95
	% Live	0.95
	% Terrestrial	0.29
GIWA	Residual Height	0.96
	% Live	0.96
	% Terrestrial	0.30

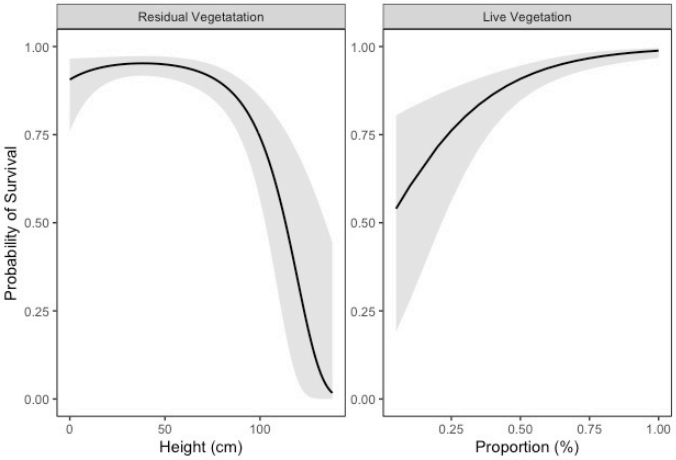

Figure 3.4. Effect plots representing parameters from the top microhabitat nest survival model for all harrier nests (n = 77) across Suisun Marsh, CA from 2017–2019. The effects of residual vegetation height (left) and proportion of live vegetation (right) on the probability of nest survival are shown. Shaded areas represent 85% CI.

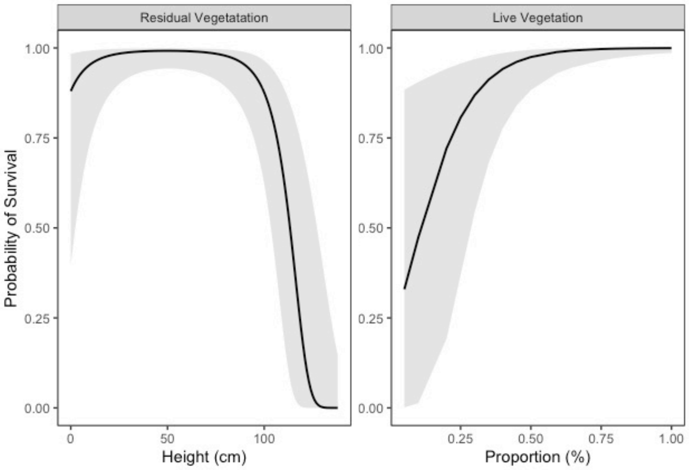

Figure 3.5. Effect plots representing parameters from the top microhabitat nest survival model for all harrier nests (n = 53) on Grizzly Island Wildlife Area only in Suisun Marsh, CA from 2017–2019. The effects of residual vegetation height (left) and proportion of live vegetation (right) on the probability of nest survival are shown. Shaded areas represent 85% CI.

3.4 Macrohabitat Nest Success

Summary statistics for macrohabitat nest site characteristics can be found in Table 2.7, Chapter 2. After stage one analyses, only distance to rose, as well as spring small mammal density at 1 km^2, and habitat type were selected for stage two of the Suisun-wide analysis. No variables from the landscape features model class (distance to water, roads, structures, or trees) were selected in stage one. The top model that predicted nest survival in the vegetation model class contained the linear form of distance to rose (β = -0.59, % CI = -0.94 to -0.28) with probability of nest survival having a negative correlation with distance to rose (Table 3.5, Fig. 3.6 A) and a cumulative weight of evidence of 0.97 (Table 3.6). Spring small mammal density at 1 km^2 was a strong, positive predictor of nest survival (β = 0.57, % CI = 0.20–1.04, Table 3.5, Fig. 3.6 B), with a cumulative weight of evidence of 0.87 (Table 3.6). Habitat type was also a strong predictor of nest survival (managed marsh β = 4.75, % CI = 4.19–1.55, Table 3.5), with a cumulative weight of evidence of 0.86 (Table 3.6). Probability of nest survival was higher when nests were in managed marsh compared to tidal marsh or upland fields (Fig. 3.6 C). All three variables from stage two were tested in global model combinations, and the top model contained linear forms for distance to rose (β = -0.53, % CI = -0.88 to -0.22) and spring small mammal density at 1km^2 (β = 0.46, % CI = 0.09 to 0.90, Table 3.5). The cumulative weights of evidence for rose and small mammal density were 0.70 and 0.69, respectively (Table 3.6). There was a negative correlation between distance to rose and nest survival, and a positive correlation between small mammal density and nest survival (Fig. 3.7). Habitat type had a cumulative weight of evidence of 0.40 (Table 3.6) but was not included in the top model.

On GIWA, the variables selected for stage two analyses were also distance to rose, spring small mammal density at 1km^2, and habitat type. No variables from the landscape features model class (distance to water, roads, structures, trees, or ATV tracks) nor the competition model class (distance to stick nests or other harrier nests) were selected in stage one. The top model that predicted nest survival for the vegetation class contained the linear form of distance to rose (Table 3.5) with a cumulative weight of evidence of 0.81 (Table 3.6). Probability of nest survival was negatively correlated to distance from rose (β = -0.67, % CI = -1.31 to -0.21, Fig. 3.8 A). Habitat type (managed marsh β = 4.96, % CI = 4.26–5.97, Fig. 3.8 B) and small mammal density at 1km^2 (β = 0.99, % CI = 0.08–4.20, Fig. 3.8 C) were also strong predictors of nest survival (Table 3.5), with cumulative weights of evidence of 0.78 and 0.85, respectively (Table 3.6). Probability of nest survival was higher when nests were in managed marsh compared to upland fields (there is no tidal marsh on GIWA). All three variables from stage two were then tested in global model combinations. The top global model that predicted nest survival contained spring small mammal density at 1km^2 (β = 0.83, % CI = 0.14–1.94) and habitat type (managed marsh β = 5.01, % CI = 4.24–6.14, upland β = -1.37, % CI = -2.90 to -0.26, Table 3.5). The cumulative weights of evidence for small mammal density and habitat type were 0.64 and 0.53, respectively (Table 3.6). There was a positive correlation between small mammal density and nest survival, and survival was significantly higher in managed marsh than upland fields (Fig. 3.9). Distance to rose had a cumulative weight of evidence of 0.43 (Table 3.6) and was not included in the top model.

The estimated daily survival rates from the Suisun and GIWA marginal (fixed effects only) global models were 0.97 for both, respectively, with an overall nest survival probability of 0.12.

In our post-hoc analysis, we found an overall positive correlation between distance to rose and quadratic average vegetation height for both Suisun (Fig. 3.10 A) and GIWA (Fig. 3.10

B) analyses. Average vegetation height was compared to average visual obstruction in both analyses because they were collinear, and height was the top predictor each time (Table 3.7). The weight of evidence for vegetation height was 1.00 (Table 3.7). In the GIWA analysis, distance to other harrier nests was not a selected predictor variable.

Table 3.5. Macrohabitat nest survival model sets for harrier nests at different spatial scales in Suisun Marsh, CA from 2017-2019.

Model sets represent all competing logistic-exposure models within 2 AIC$_c$ scores of the top model for all model combinations.

Spatial Scale and Model Class	**Model**	***K***	**–2(*L*)**	**AIC$_c$**	**ΔAIC$_c$**	**ω_i**
Suisun						
Vegetation	Rose	1	-100.75	207.57	0.00	0.66
	Rose^2	2	-100.49	209.10	1.53	0.31
Habitat	Habitat	1	-100.86	209.82	0.00	0.86
Prey	Small Mammal Density 1km$^{2\text{-}1}$	1	-102.05	210.17	0.00	0.63
	(Small Mammal Density 1km$^{2\text{-}1}$)^2	2	-102.00	212.11	1.94	0.24
Global	Rose + Small Mammal Density 1km$^{2\text{-}1}$	2	-99.10	206.31	0.00	0.35
	Rose	1	-100.75	207.57	1.26	0.19
	Habitat + Small Mammal Density 1km$^{2\text{-}1}$	2	-98.75	207.66	1.35	0.18
GIWA						
Vegetation	Rose	1	-50.98	108.06	0	0.59
	Rose^2	1	-50.91	110.01	1.94	0.22
Habitat	Habitat	1	-50.84	107.79	0.00	0.78
Prey	Small Mammal Density 1km$^{2\text{-}1}$	1	-50.79	107.69	0.00	0.55
	(Small Mammal Density 1km$^{2\text{-}1}$)^2	2	-50.37	108.92	1.22	0.30
Global	Habitat + Small Mammal Density 1km$^{2\text{-}1}$	2	-49.24	106.67	0.00	0.24
	Rose + Small Mammal Density 1km$^{2\text{-}1}$	2	-49.60	107.39	0.72	0.17
	Small Mammal Density 1km$^{2\text{-}1}$	1	-50.79	107.69	1.02	0.15
	Habitat	1	-50.84	107.79	1.12	0.14
	Rose	1	-50.98	108.06	1.40	0.12

Table 3.6. Cumulative AIC$_c$ weights of evidence ($\sum \omega_i$) of macrohabitat nest survival model parameters for harrier nests at different spatial scales in Suisun Marsh, CA from 2017-2019.

Spatial Scale and Model Class	**Model Parameters**	$\sum \omega_i$
Suisun		
Vegetation	Rose	0.97
Habitat	Habitat	0.86
Prey	Small Mammal Density 1km$^{2-1}$	0.87
Global	Rose	0.70
	Small Mammal Density 1km$^{2-1}$	0.69
	Habitat	0.40
GIWA		
Vegetation	Rose	0.81
Habitat	Habitat	0.78
Prey	Small Mammal Density 1km$^{2-1}$	0.85
Global	Habitat	0.74
	Small Mammal Density 1km$^{2-1}$	0.64
	Habitat	0.53
	Rose	0.43

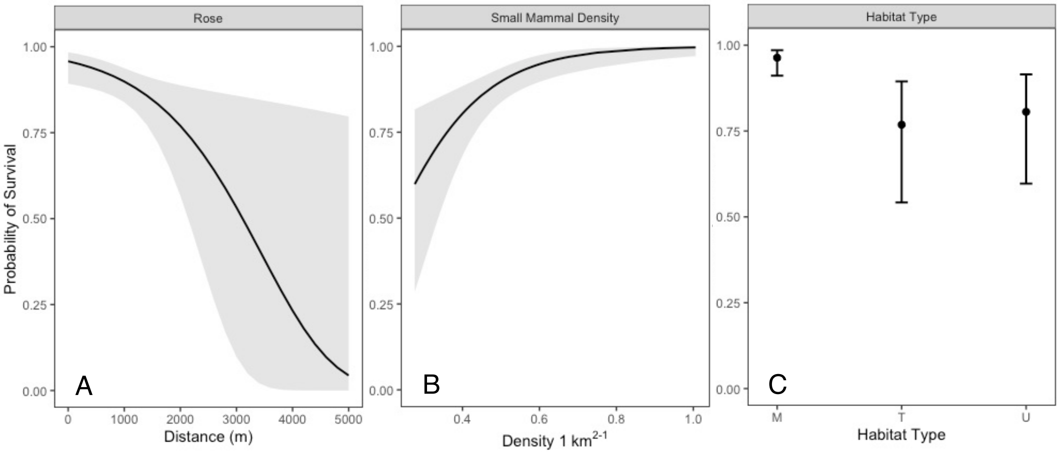

Figure 3.6. Effect plots representing parameters from the top landscape (A), prey (B), and habitat type (C) nest survival models for all harrier nests (n = 77) across Suisun Marsh, CA from 2017–2019. The effects of distance to rose (A), small mammal density 1 km$^{2-1}$ (B), and habitat type (C) on the probability of nest survival are shown. Shaded areas and error bars represent 85% CI.

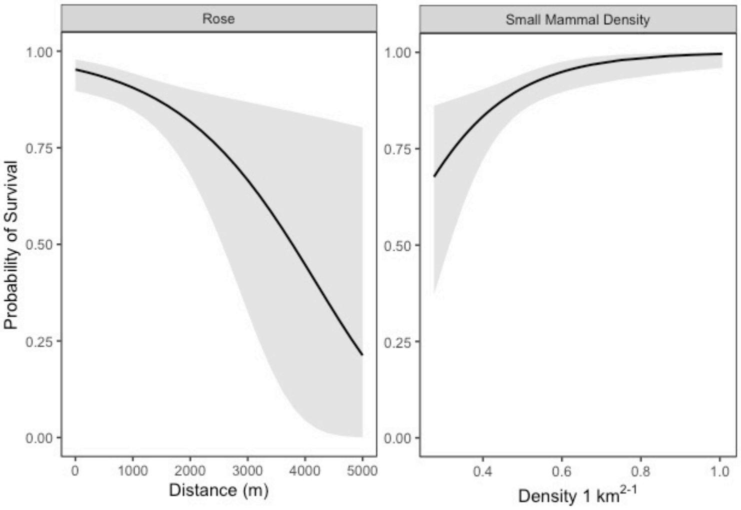

Figure 3.7. Effect plots representing parameters from the top global nest survival model for all harrier nests (n = 77) across Suisun Marsh, CA from 2017–2019. The effects of distance to rose (left) and small mammal density 1 km$^{2-1}$ (right) on the probability of nest survival are shown. Shaded areas represent 85% CI.

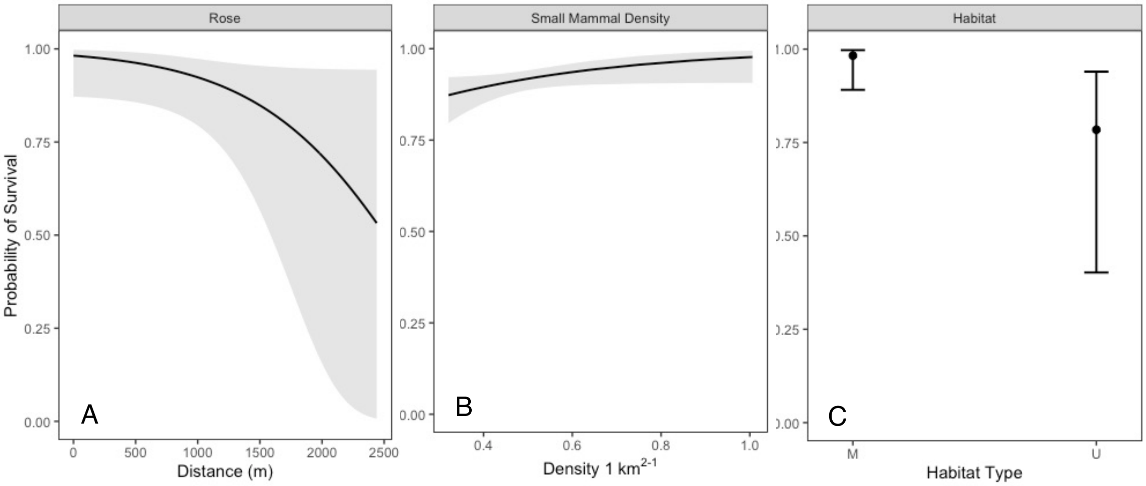

Figure 3.8. Effect plots representing parameters from the top landscape (A), prey (B), and habitat type (C) nest survival models for all harrier nests (n = 53) on Grizzly Island Wildlife Area only in Suisun Marsh, CA from 2017–2019. The effects of distance to rose (A), small mammal density 1 km$^{2-1}$ (B), and habitat type (C) on the probability of nest survival are shown. Shaded areas and error bars represent 85% CI.

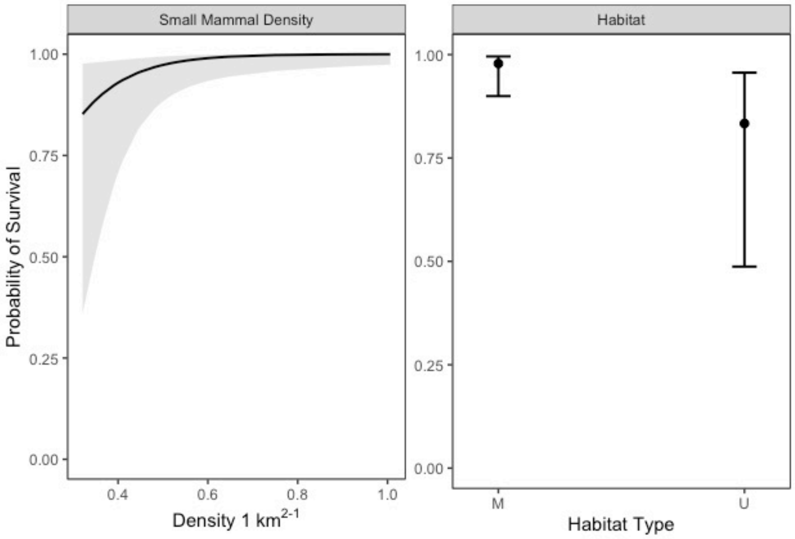

Figure 3.9. Effect plots representing parameters from the top global nest survival model for all harrier nests (n = 53) on Grizzly Island Wildlife Area only in Suisun Marsh, CA from 2017–2019. The effects of small mammal density 1 km^{2-1} (left) and habitat type (right) on the probability of nest survival are shown. Shaded areas and error bars represent 85% CI.

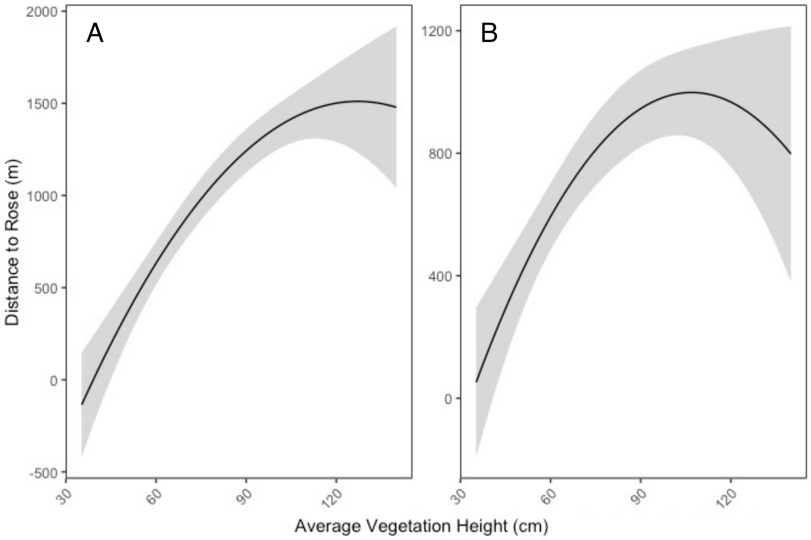

Figure 3.10. Effect plots from the post-hoc analysis representing the relationship between distance to rose and average vegetation height for harrier nests across A) Suisun March and B) Grizzly Island Wildlife Area, CA from 2017–2019. Shaded areas represent 85% CI.

Table 3.7. Post-hoc distance to rose model sets including beta coefficients and 85% confidence intervals for harrier nests at different spatial scales in Suisun Marsh, CA from 2017-2019. Model sets represent all competing linear regression models within 2 AIC_c scores of the top model for all model combinations.

Spatial Scale	**Model**	***K***	**–2(*L*)**	**AIC_c**	**ΔAIC_c**	**ω_i**	**β**	**85% CI**
Suisun	Average Vegetation $Height^2$	2	-462.05	932.22	0.00	1.00	-0.12	-0.17 to -0.06
GIWA	Average Vegetation $Height^2$	2	-334.57	677.30	0.00	1.00	-0.16	-0.26 to -0.06

4. Discussion

Despite their ubiquity across North American wetland and grassland ecosystems, targeted research investigating factors influencing nest success in Northern Harrier breeding populations have been limited to just a handful of studies, with only two occurring within the past two decades (Hamerstrom et al. 1985, Simmons and Smith 1985, Toland 1985, 1986; Simmons et al. 1986b, a; Barnard et al. 1987, Dechant et al. 1998, Evrard and Bacon 1998, Vukovich and Ritchison 2006, Datta 2016). Our research represents the first targeted study investigating factors influencing harrier nest success in California and in Suisun Marsh, which is an important harrier breeding site (Shuford and Gardali 2008). Overall, apparent nest success in our study was 40% (range = 29–53%), which is within the range of apparent nest success reported in other populations. Apparent nest success is variable across studies, ranging from 22% to 75% (Hammond and Henry 1949, Sealy 1967, Duebbert and Lokemoen 1977, Hamerstrom 1979, Thompson-Hanson 1984, Simmons and Smith 1985, Toland 1986, Kantrud and Higgins 1992, Evrard and Bacon 1998, Vukovich and Ritchison 2006, Datta 2016, Supplemental Table 3.1), and success is highly variable across years within the same study, with extremes reported of 0–100% (Sealy 1967). Nest success in our population, however, may not be comparable to other studies since there is a wide range of inconsistent success statistics reported, like fledging (number of nests that fledge at least one young/total hatched nests) or hatching success (number of nests that hatch/total nests), or even the percent of eggs that fledge or hatch out of the total number of eggs, and not nests (Supplemental Table 3.1).

Incidental nest monitoring in Suisun from 1987–1992 that occurred concurrently with waterfowl nest research found overall Mayfield nest survival to be 21% (range = 18–38%) (Loughman and McLandress 1994), which is comparable to our overall Mayfield nest survival rate of 18% (range = 5–26%). Loughman and McLandress (1994) also reported an average clutch size of 4.6 (*n* = 119, range = 3–7), which is comparable to our average clutch size of 4.3 (*n* = 77, range = 1–6). However, the number of nests and nest density have significantly declined in Suisun over the past three decades (Chapter 2, Loughman and McLandress 1994). Taken together, these results suggest overall nest success and clutch sizes are relatively stable in Suisun, but population size has decreased, and nest success may be lower than most populations outside of California. Further, using the daily survival rates calculated from the logistic-exposure method across all marginal global top models, we estimate overall nest survival to vary from just 0.3% (Suisun) to 50% (GIWA) accounting for microhabitat, and 12% for both Suisun and GIWA accounting for macrohabitat, prey density, and habitat type. Loughman and McLandress (1994) did not investigate factors that influenced nest success making it difficult to compare causal factors for low nest success in Suisun. Regardless, nest success is low in our study as compared to other populations, and changes in microhabitat, macrohabitat, prey densities, and habitat type may all contribute to this decline since they are top predictors of nest success and are associated with low overall survival probabilities.

A decline in California voles is of particular interest because we know voles have a strong positive influence on clutch sizes, number of nests, number of breeding individuals, and nest success in harrier populations elsewhere (Hamerstrom 1979, Hamerstrom et al. 1985, Simmons et al. 1986b). These metrics are also highly influenced by polygyny and male provisioning rates (Hamerstrom et al. 1985, Simmons et al. 1986a, Simmons 1988), but we were unable to monitor individual males to determine polygyny and we did not record provisioning rates in this study. Small mammal populations in our study, particularly voles, are alarmingly low. Ackerman (2002) captured a total of 2,863 small mammals, 469 of which were voles, across a three-year (1998–2000), two-season (spring and summer) study period using the same grid size, traps, bait, trap nights, and sampling some of the same fields sampled in our study in Suisun. By contrast, we captured 1,318 small mammals, only 28 of which were voles. A key difference between our two studies is that we sampled across habitat types, with only four grids in upland habitat, whereas Ackerman (2002) sampled six (1998–1999) to ten (2000) grids in upland habitat only. Because of this we are unable to directly compare abundance and density estimates between studies, but this difference represents a 17-fold decrease in total individual voles captured. Further, if we compare the number of harrier nests found in upland fields from 1987–1992 (n = 119) with only the number of nests from the same upland fields in our study (n = 20), this represents a 6-fold decrease. Though a direct correlation between vole populations and the number of nests cannot be made in our study, these declining trends suggest a relationship may exist. Additionally, researchers monitoring long-term population trends of the endangered Salt Marsh Harvest Mouse in Suisun have reported very low vole captures and these lows have been observed for longer periods of time than expected for the typical three-year vole cycles (L. Barthman-Thompson, CDFW, personal communication).

Voles were the most common species captured in 1998 and 2000 and were the most influential species on and were positively correlated with Mallard (*Anas platyrhynchos*) nest success (Ackerman 2002). A suite of hypotheses were tested to understand this relationship, and the only one with support was the indirect effects of coexisting prey hypothesis, which states that predator species of both waterfowl nests and voles will preferentially chose voles when populations are highly abundant (Ackerman 2002). Spring small mammal densities were also found to have a positive effect on the number of fledglings (Fig. 1) and overall nest success (Table 5, Fig. 7, 9) in our study. Though vole captures were very low in our study, the general population trend across years was similar for voles and other small mammal species, making it likely that small mammal density and abundance estimates, and their effects on breeding harriers, are a proxy for vole populations. Given what we know about the importance of voles on both harrier and waterfowl nest success, understanding the reasons for vole population declines is a key missing component to informing habitat and wildlife population management in Suisun.

That we found spring small mammal density to influence clutch size is not surprising since females do not hunt during the early nesting season and males provide all prey (Martin 1987, Simmons et al. 1987, Vukovich and Ritchison 2006). However, spring and not summer small mammal density influenced nest survival, which does not support our original hypothesis. This result suggests that either male provisioning in the early nesting season has a bigger impact on nest success overall or that females may provision different prey items to nestlings and small mammals are not as important at the end of the nesting season. Females begin hunting and provisioning young after nestlings are two to three weeks old (Martin 1987, Vukovich and Ritchison 2006). It is at this time that males may also reduce provisioning or completely abandon nests all together (Simmons et al. 1987). There is evidence of prey size differences between males and females in many raptor species, and that females generally provision larger prey items to nestlings (e.g., Marquiss 1980, Pierce and Maloney 1989, Panter and Amar 2021). Indeed, this is even one hypothesis for reverse sexual size dimorphism in raptors (Olsen and Olsen 1987, Slagsvold and Sonerud 2007, Pande and Dahanukar 2012). In Hen Harriers (*Circus cyaneus*) with a polygynous mating system, there is evidence that secondary females can account for reduced male provisioning by capturing and provisioning their young with larger prey items than primary females (Redpath et al. 2006). However, at least one study found no difference between prey sizes provisioned by male and female Northern Harriers (Vukovich and Ritchison 2006), and studies in other raptor species have found no differences, as well (Cardador et al. 2012, Sonerud et al. 2013). In our population, we anecdotally observed female harriers capture and provision very large prey items to nestlings, including Ring-necked Pheasant (*Phasianus colchicus*) and American Bittern (*Botaurus lentiginosus*) nestlings, as well as large snakes that we did not observe males capture, but we were not able to quantify these differences for formal analysis. Diversity and abundance of prey species appears to be one driving factor in differences in prey sizes between males and females. For example, while there were no differences between prey sizes captured by male and female Marsh Harriers (*Circus aeruginosus*), females provisioned five times as much biomass as males, which could account for seasonally reduced availability of larger prey items (Brzeziński and Zmihorski 2009). Likewise, male Northern Harriers have displayed prey switching from small mammals to birds across the nesting season as prey abundance changes (Martin 1987), and harriers may even time nesting with the availability of more easily obtainable passerine nestlings later in the nesting season, though voles are still the most important and primary prey item in the early nesting season (Barnard et al. 1987). Identifying prey species on nest cameras coupled with observations of prey deliveries outside of the nest could reveal shifts in prey species across the nesting season, which prey species are seen to be captured by males and females (Sonerud et al. 2013), and lead to more refined understanding of the effects of prey on nest success in Suisun.

Looking at habitat type, we found nests in managed marshes (semi-wet) to have significantly higher nest success than nests in either tidal marsh (very wet) or upland fields (dry). Simmons and Smith (1985) found that the best predictors of harrier nest success were water and emergent wetland vegetation at the nest. Both wet nest sites and emergent vegetation may prevent predators from accessing nests better than dry sites in woody shrub habitat. Indeed, harriers nesting in dry reclaimed grasslands have low overall nest success (22%) believed to be caused by a more diverse predator community and higher vulnerability to nest discovery and access (Vukovich and Ritchison 2006). At the U.S. Department of Energy Hanford Site in south-central Washington, Thompson-Hanson (1984) also found nest success to be three times higher at wet sites than dry sites. Though we did not find a direct effect of water or vegetation density on nest success, managed marshes represent habitat with a more complex distribution of water on the landscape due to spring draw downs, allowing harriers to select nest sites at a preferred distance from water. Indeed, distance to water was a significant predictor of nest site selection in Chapter 2, where harriers selected nest sites closer to water than other landscape variables suggesting a possible predator defense selection mechanism.

Tidal marsh habitat, while limited in disturbance and containing the densest vegetation, is prone to catastrophic flooding events due to “King Tides”, which is the highest high tide of the year occurring in late May due to a new or full moon in perigean orbit, also known as the perigean spring tide. These King Tides correlated to the median hatch date of 22 May each year, leaving nearly-hatched eggs and newly-hatched nestlings vulnerable to exposure and drowning. Indeed, only nests that were initiated early in the nesting season could survive the King Tide because nestlings were old enough to stand up above the waterline and withstand exposure to water for prolonged periods of time (personal observation). Tidal marsh in Suisun today is also geomorphically different from historical natural tidal marsh, with narrow strips of remnant marsh between manmade levees and open bays and sloughs that provide little elevational gradient to diffuse tidal inundation. As a result, normal tide cycles and flooding events from King Tides are extreme and could essentially render tidal marsh habitat as ecological traps for nesting harriers and other wildlife alike (e.g., Overton et al. 2014, Reynolds et al. 2015, Hunter 2017, Ma et al. 2019, Thorne et al. 2019). Coupled with the pressures of sea-level rise, sedimentation, and subsidence, restoring large patches of tidal marsh habitat in Suisun that can diffuse he effects of high tides across the tidal plane is critical to protecting this sensitive and important habitat and increasing flood protection for the rest of Suisun (Siegel et al. 2010, SMP 2013).

Whereas tidal marshes may be too wet, upland fields are very dry throughout the nesting season and had the highest frequency of predation in this study. Distance to ATV tracks, which primarily occur in upland fields, was not a top predictor of nest success on GIWA, but harriers do select nest sites farther from ATV tracks (Chapter 2), suggesting an avoidance of human disturbance and/or predators using ATV tracks as movement corridors. Harrier nests were also more often placed in managed marsh habitat, followed by tidal marsh habitat, and lastly upland habitat despite tidal marsh representing only 10% of available habitat compared to 30% available upland habitat (Chapter 2). These results combined indicate harriers are selecting wet sites more often than dry sites, and non-tidal wet sites result in the highest nest success. Managed marsh habitat may represent a balance between the near complete predator defense of very wet, tidal marsh habitat and the very high predation risks of dry, upland habitat.

We also found support for height of residual vegetation and proportion live vegetation at the nest affecting nest success, with higher nest survival probabilities at ≤ 100 cm tall residual vegetation and increased proportion of live vegetation. In Wisconsin and Missouri, nest success was positively correlated with proportion of residual vegetation, but negatively correlated with proportion live vegetation (Toland 1986, Evrard and Bacon 1998). Increased proportion of residual vegetation has been found to be important for harrier nest site selection, as well (Clark 1972, Duebbert and Lokemoen 1977, Hamerstrom and Kopeny 1981, Apfelbaum and Seelbach 1983, Kantrud and Higgins 1992). That our study found higher proportions of live vegetation rather than residual vegetation to influence nest success is potentially an artifact of our sampling protocol. We collected nest habitat characteristics at the end of the nesting season to limit disturbance during incubation, whereas most other studies collected these data at initial nest discovery. We recognize that our protocol could be biasing our microhabitat results, especially proportion live vegetation since live vegetation grows across the nesting season whereas residual vegetation does not (McConnell et al. 2017). Thus, this measurement could be masking the effect of proportion residual vegetation. Indeed, proportion residual vegetation was selected as a predictor in stage two of the Suisun-wide analysis but was not selected in the global model. Since the height of residual vegetation often correlates to the proportion of residual vegetation at the nest, our results suggest that at least the presence of residual vegetation at the nest is important in nest success, which is consistent with other studies.

At the Suisun-wide scale, distance to California Rose (*R. californicus*) was positively correlated to nest success. We expected that the proportion of rose, and not distance to rose, would influence nest success since proportion of rose at the nest was important for nest site selection (Chapter 2). In our post-hoc analysis, we found an overall positive correlation between distance to rose and average vegetation height. It is possible that nests near rose simply benefit from increased protection from nearby rose brambles, reducing the need to select very tall vegetation at the nest. Thus, nests near rose enjoy higher nest success regardless of microhabitat characteristics at the nest. Alternatively, if these nests belong to secondary females, they may either be lower quality nest sites or benefit from group nest defense from nearby harriers at semicolonial nesting sites (Kitowski 2008, Krupiński et al. 2010) also reducing the need for tall vegetation at the nest. However, we did not find semicolonial nesting to be related to distance to rose, and nest success differences between primary and secondary females in another harrier population were best explained by male provisioning rates and not nest site quality (Simmons and Smith 1985, Simmons et al. 1986a). Further, Simmons (1983) found no evidence of group nest defense in semicolonial nest sites. Because our breeding population is small and small mammal populations, particularly voles, were low across all three years of our study, polygyny may not have even occurred in our population (Hamerstrom et al. 1985, Simmons et al. 1986b). As such we are not able to determine the relationship between habitat quality and polygyny in this study. It is clear that rose plays an important role in both nest site selection (Chapter 2) and nest success in Suisun, but more research investigating how proximity to rose influences nest success is needed.

Lastly, we found no differences between nest success in early vs. late initiating nests, nor between any other measures of nest timing in our study. The lack of support for effects of observation or nest age on nest success suggests that our nest visit schedule did not affect daily nest survival or overall nest success (Crimmins et al. 2016). Barnard (1987) found that early initiated nests had higher nest success than later initiated nests in a harrier breeding population in New Brunswick, Canada. However, this population also had a high prevalence of polygyny that could explain this difference (Simmons et al. 1986b, a). As previously described, our study population was small and vole populations were low. If these two factors influence polygyny in our study population like they do elsewhere, it is possible that polygyny did not occur at our study site and differences in nest initiation were not a result of female settling order, and thus nest success was not affected by differences in male provisioning rates.

5. Management Implications

Given the importance of voles to the breeding ecology of harriers and waterfowl alike in Suisun, management plans for these nesting species should include concurrent long-term small mammal monitoring. Targeted research focusing on vole populations, specifically investigating their breeding and foraging ecology to better understand their population cycles is necessary to improve habitat management across Suisun. Investigating any habitat management and vegetation species changes that may have occurred over time in Suisun is a good first step to understanding possible changes to vole populations, as well. Voles typically respond positively to similar habitat management strategies that harriers respond to, including limiting vegetation and ground disturbance (i.e., mowing, burning, discing, etc.) in upland habitats for at least two years (Dechant et al. 1998, Slater and Rock 2005, and references therein). Minimizing disturbance to habitat will also serve to provide more residual vegetation for nesting harriers. California Voles exhibit shifts in their diet across seasons and may also have specific vegetation species requirements for foraging at different times of the year (Batzli and Pitelka 1971). Determining these preferences will improve habitat management to better support vole populations in Suisun. California Rose is especially important for harriers in Suisun, and managers should avoid trimming or removing rose if possible and allow it to expand naturally. Lastly, tidal marsh restoration that incorporates larger areas (> 100 ha, Toland 1986, Kantrud and Higgins 1992) and numerous smaller channels to better diffuse the effects of high tides across the tidal plane could reduce nest flooding for harriers and other sensitive tidal marsh species in Suisun.

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between USGS and CDFW, and IACUC protocol # 19806. Use of trade, product or firm names does not imply endorsement by the U.S. Government.

Supplemental Material

Supplemental Table 3.1. Summary of nest success statistics reported across harrier studies, including study name, sample size (number of nests unless otherwise noted), total apparent nest success across study years (number of successful nests unless otherwise noted), Mayfield's nest success (unless otherwise noted), and study location. The success type represents apparent nest success as either hatching success (number of nests that hatched at least one egg/total number of nests) or fledging success (number of nests that fledged at least one young/total number of nests). Some studies reported hatching and fledging success as the number of eggs that hatched or fledged/total number of eggs. These success types are denoted as "hatched eggs" or "fledged eggs."

Study	Sample Size	Apparent Nest Success	Success Type	Mayfield's Nest Success	Location
This Study	77	40% (31)	Fledged	18%	California, USA
Hammond and Henry 1949	60	72% (43)	Hatched	-	North Dakota, USA
		68% (41)	Fledged		
Sealy 1967*	11 (49 eggs)	57% (28 eggs)	Hatched Eggs	-	Alberta, Canada
		75% (21 eggs)	Fledged Eggs		
	21 (85 eggs)	62% (58 eggs)	Hatched Eggs	-	Saskatchewan, Canada
		67% (39 eggs)	Fledged Eggs		
Duebbert 1977	20	65% (13)	Hatched	-	South & North Dakota, USA
Hamerstrom 1979	172	74% (128)	Hatched	-	Wisconsin, USA
Thompson-Hanson 1984	30	43% (13)	Fledged	-	Washington, USA
Simmons and Smith 1985	64	83% (53)	Fledged	-	New Brunswick, Canada
Toland 1986*	15 (79 eggs)	70% (55 eggs)	Hatched Eggs	-	Missouri, USA
		60% (55 eggs)	Fledged Eggs		
Kantrud and Higgins 1992	112	61%	Hatched	41%**	South & North Dakota, Montana, USA Manitoba, Canada

Loughman and McLandress 1994	135	-	-	21%***	Suisun Marsh, California, USA
	40	-	-	28%***	San Joaquin Valley, California, USA
	20	-	-	18%***	Sacramento Valley, California, USA
	36	-	-	16%***	Northeastern California, USA
Evrard and Bacon 1998	17	35% (6)	Hatched	-	Wisconsin, USA
Vukovich and Ritchison 2006	46	22% (10)	Fledged	-	Kentucky, USA
Datta 2016	22	45% (10)	Fledged	-	North Dakota, USA

* These studies reported hatching success as a percent of eggs that hatched out of the total number of eggs across all nests. Fledging success is calculated as the percent of hatched eggs that fledged across all nests.

** Calculated using the Discrete version (Johnson 1991) of the Green (1989) estimator for nest success, not Mayfield’s.

*** Calculated using Mayfield’s-40% method (Miller and Johnson 1978).

Chapter 4. Migration and Habitat Selection Characteristics of Northern Harriers (*Circus hudsonius*) Wintering in Suisun Marsh, California

Abstract

Little is known about Northern Harrier (*Circus hudsonius*) migration timing and routes, or habitat selection across their annual cycle, particularly at stopover sites during migration and on wintering areas. We used lightweight GPS/GSM solar-powered transmitters to study migration and habitat selection of adult female Northern Harriers wintering in Suisun Marsh, California. We recorded a total of 18 spring and 11 fall complete (round-trip) and partial (one-way) migrations for 14 individual harriers and identified nest sites across five Western United States (CA, WA, OR, ID, AK). We also recorded the three longest-distance migrations for any harriers to date across two individuals breeding in Alaska, ranging from 13,000 to nearly 20,000 km traveled roundtrip. Of the 11 fall migrations recorded, all birds returned to Suisun Marsh highlighting its importance in Northern Harrier wintering ecology in Western North America. Spring migration was shorter than fall migration by nearly two months, with fewer stopovers and a faster migration speed (~ 200 km d^{-1}) suggesting strong selection pressure to reach the breeding grounds early. Migration timing is generally consistent with known timing from raptor migration monitoring stations across North America. Migration routes were primarily along central and eastern corridors through California, Washington, and Oregon, and generally continued along inland intermountain regions through British Columbia and into Alaska for long-distance migrants. Wetland habitat was the most consistently selected habitat type across the annual cycle, with grassland and shrubland habitat also selected at stopover locations, and cultivated habitat surrounding Suisun Marsh also selected in the winter. Many breeding areas and stopover locations occurred on protected state and federal lands. Raptor migration monitoring and banding

stations located throughout Western North America may be misaligned with harrier migration, leading to low detections and population estimates. Focusing migration monitoring along wetland habitat corridors and increasing breeding population research on protected lands could improve Northern Harrier management and conservation efforts.

1. Introduction

Northern Harriers (*Circus hudsonius*; hereafter "harriers") are an understudied yet ubiquitous raptor species found across North America. Though widespread, harriers have experienced population declines across their range primarily due to habitat loss (Smith et al. 2020). Harriers are well-known breeders in wetland habitat and are generally considered wetland and grassland habitat specialists (Chapter 1, Smith et al. 2020). However, little is known about their habitat selection across their annual cycle, particularly at stopover sites during migration and on wintering areas. Even less is known about their migration timing and routes, and spring and fall migration are two high risk periods in a birds' annual cycle that may contribute significantly to survival and reproductive success in the breeding season (Faaborg et al. 2010). Understanding full annual cycle migration ecology is crucial to developing more robust and complete conservation plans for a sensitive and declining species like harriers (Mehlman et al. 2005, Shuford and Gardali 2008).

In raptors, migration has been the focus of extensive research, primarily through migration monitoring stations (also known as hawk watches) and band recoveries (Goodrich and Smith 2008). Relatively few species have been monitored using telemetry, and these are mostly large raptors that can handle the weight of VHF and satellite transmitters (Goodrich and Smith 2008). Harriers are no exception, and almost all research investigating their migration has been conducted using migration monitoring stations, band recoveries, and observations at breeding and wintering areas (e.g., Bildstein et al. 1984, Mindell and Mindell 1984, Bernarz et al. 1990, Titus and Fuller 1990, Pavelka et al. 1992, Niles et al. 1996, Mueller et al. 2000, Smith et al. 2008, Schimpf et al. 2020, Smith et al. 2020 and references therein). Further, almost all harrier migration studies have been conducted in the Midwest and Eastern portions of North America, with only a couple of studies having been conducted in the West (Beske 1982, Mindell and Mindell 1984). Even fewer studies have used telemetry to study harrier migration: one formal study investigated juvenile harrier migration in Wisconsin using VHF telemetry in the late 1970s (Beske 1982), while another study conducted by the Avian Research and Conservation Institute and the U.S. Fish and Wildlife Service in Florida deployed satellite transmitters on harriers in 2010 and 2012, yet no publication of their findings exists to date (ARCI 2017).

Harriers are believed to be partial migrants, with some individuals of a population migrating while others remain resident on the breeding grounds year-round (Goodrich and Smith 2008). Additionally, harriers breeding at more northern latitudes may winter on the same breeding grounds as summer breeders that may migrate out after breeding, such that breeding and wintering ranges overlap between populations (Goodrich and Smith 2008). This can make identifying and protecting individual populations challenging. Low detection at known raptor migration sites relative to other species indicates that migratory individuals are also thought to be "broad-front" migrants whereby individuals spread out and migrate across vast landscapes instead of along well-defined corridors or coastlines (Goodrich and Smith 2008, Smith et al. 2020). Unraveling this complicated migratory behavior can help improve focused conservation efforts for harrier metapopulations as a whole and at specific locations along migratory routes.

Recent advances over the past decade in transmitter technology have allowed for increased migration studies in smaller, lesser-studied raptor species (e.g., Javed et al. 2012, Limiñana et al. 2015, Linkhart et al. 2016). These same advances have allowed this study to be the first to describe detailed migration ecology and habitat selection of harriers in North America using fine-scale location data collected using GPS/GSM transmitters. Discovering migratory routes and stopover locations, migration timing, habitat selection, and site fidelity of migrating harriers will help managers identify important areas and habitats across their annual cycle that are crucial to their conservation and management in the future (Faaborg et al., 2010a).

2. Methods

2.1 Study Area

This study was conducted in Suisun Marsh, CA on the Grizzly Island Wildlife Area (GIWA) and surrounding private duck hunting clubs and properties owned by non-profit organizations (38.1515° N, 121.9717° W; see detailed description in Chapter 2, Fig 2.1 Chapter 2).

2.2 Capture and Transmitter Deployment

We targeted adult female harriers wintering in Suisun for this study. Capture techniques for wintering harriers have been described in detail in Chapter 1 of this dissertation. As a summary, wintering individuals were captured across three winter seasons (Jan–Feb 2018, Dec 2018–Mar 2019, and Dec 2019–Jan 2020) using noose carpets and remote-triggered bow nets baited with waterbird carcasses (i.e., American Coots, *Fulica americana*, and various waterfowl species). We targeted adult females for this study as they are most abundant across our study site and seasons, are easiest to capture, and were large enough for transmitters used in this study (transmitters with harnesses weighed less than or equal to ~ 3% body weight). We used Crex GPS/GSM transmitters (14 g, Ecotone, Poland) in the first winter season, and OrniTrack-10 GPS/GSM transmitters (10 g, Ornitela, Lithuania) in the second and third winter seasons. All transmitters were attached with a backpack mounted harness design made of Teflon. All captured birds were measured for morphometrics (wing chord, tail length, tarsus depth, culmen length, hallux length, and weight) and banded with a USGS aluminum lock-on leg band.

All trapping and transmitter attachment was conducted under federal banding permit #23947, California scientific collection permit #8090, and IACUC protocol #19781.

2.3 Migration, Stopover Locations, and Nest Sites

We determined migration to begin on the first date harriers made directed straight-line movements in either a northerly (Spring) or southerly (Fall) trajectory away from (> 1 degree change in latitude) either their wintering or breeding grounds, respectively. Stopover locations were determined by areas where harriers spent > 24 hrs stopped at a localized longitude and latitude and were only areas that occurred along the migration route (i.e., not areas used within the breeding area but outside of the nest site). Breeding and wintering areas were determined by the first date of arrival at a consistent longitude and latitude where harriers remained for several months (typically within the same degree of longitude and latitude). Nest locations within breeding areas were determined by repeated locations at the same exact coordinates during the nesting season.

We calculated total distance of migratory routes for both spring and fall using the last date a bird was at their wintering or breeding area to the first date they arrived at their breeding or wintering area (respectively), including stopovers, using the "trajr" package (McLean and Skowron Volponi 2018) in program R (version 3.6.3; R Core Team 2020). Migration speed was calculated by dividing the total migration distance by the number of migration days (km d^{-1}).

We also designated a bird as either a long- or short-distance migrant based on the median distance traveled during spring migration, which was our most complete migration recorded. Birds that travelled farther than the median distance were considered long-distance migrants, and birds that travelled less than the median were considered short-distance migrants. We used generalized linear mixed models to test for differences in migration distance, stopover duration, migration speed, arrival time, and departure time between long- and short-distance migrants across years, with bird ID as a random effect to account for repeated measures in individual birds. Long- and short-distance migrants were coded as a binomial response variable (long = 1, short = 0). We used the glmer function from the "lme4" package (Bates et al. 2015) in Program R (version 3.6.3; R Core Team 2020). We used the same two-stage modeling approach described in Chapter 2 and we repeated this analysis for both spring and fall migration.

2.4 Home Range Estimation and Habitat Selection

Home range estimation was calculated using a kernel density estimator (KDE) and specifying the reference smoothing parameter (*h*) in package "adehabitatHR" (Calenge 2006) in Program R (version 3.6.3; R Core Team 2020). We used KDE rather than a movement model (e.g., Brownian Bridge Movement Model) because not all transmitters on individual birds recorded enough locations to meet the data requirements of movement models. Using KDE allowed us to calculate comparable home ranges across birds with varying temporal location data from different transmitter types (range: 0.5-24 hr locations). We calculated 99%, 95%, and 50% KDE home ranges for nest sites and stopover locations for each bird that recorded > five locations (the minimum requirement for KDE). Nest sites were differentiated from the general breeding area by determining the first date a bird visited a nest location to the last date a bird returned to the nest location.

We then calculated the proportion of each available habitat type within each 95% KDE for each nest and stopover site for each bird by extracting the count of grid cells from the 2016 National Land Cover Database (NLCD) raster layer for the continental United States and Alaska (Wickham et al. 2021) or the 2015 North American Land Change Monitoring System (NALCMS) raster layer for Canada (Commission for Environmental Cooperation 2020), depending on where sites were located. Habitat types from the raster layers were summed into the following seven categories: wetland (emergent herbaceous wetland, woody wetland, wetland), grassland (grassland/herbaceous, sedge/herbaceous, lichens, moss, temperate or sub-polar grassland, sub-polar or polar grassland-lichen-moss), shrubland (dwarf scrub, shrub/scrub, temperate or sup-polar shrubland, sub-polar or polar shrubland-lichen-moss), cultivated (pasture/hay, cultivated crops, cropland), forest (deciduous forest, evergreen forest, mixed forest, temperate or sub-polar needleleaf forest, sub-polar taiga needleleaf forest, temperate or sub-polar broadleaf deciduous forest), open water, and other (all levels of developed land, barren land, perennial ice/snow, snow/ice, urban). We also extracted the used habitat type at each GPS/GSM location within each home range for each bird. Habitat selection was calculated using a type III resource selection function (use:availability, Manly et al 2002) by comparing the available habitat types within each individual home range to the habitats at each bird location within each home range using Chi-square tests. We also calculated global Manly selection ratios where > 1.0 indicates a positive selection (preference) and < 1.0 indicates avoidance of a particular habitat type. This analysis was conducted for each site (nest, spring stopover, fall stopover, and winter). We used the widesIII function in the "adehabitatHS" package (Calenge 2006) in Program R (version 3.6.3; R Core Team 2020). For birds with more than one stopover location for spring or fall, or with records from more than one winter or breeding season, we averaged their habitat use and availability across all home ranges for each site.

We used generalized linear mixed effect models to test for differences in home range size (99%, 95%, and 50% KDE) and habitat selection within 95% KDE home range for each habitat type between long- and short-distance migrants across years, with bird ID as a random effect to account for repeated measures of individual birds. Long- and short-distance migrants were coded as a binomial response variable (long = 1, short = 0). We used the glmer function from the "lme4" package (Bates et al. 2015) in Program R (version 3.6.3; R Core Team 2020). We used the same two-stage modeling approach described in Chapter 2 and we repeated this analysis for each site (nest, spring stopover, fall stopover, winter).

3. Results

3.1 Capture and Transmitter Deployment

We marked 33 adult females during the winter seasons; 10 females in 2018–2019 were equipped with Ecotone Crex Transmitters; 13 females in 2018–2019 and 9 females in 2019–2020 were equipped with OrniTrack-10 transmitters (one female was equipped with an Ecotone Crex Transmitter in 2018–2019). We also marked two adult males with an Ornitela OrniTrack-10 transmitter in 2019–2020 for a total of 35 individual harriers. In total, we collected 136, 371 locations at intervals ranging from 0.5-24 hr (Table 4.1).

3.2 Migration, Stopover Locations, and Nest Sites

We recorded a total of 18 spring and 11 fall complete (round-trip) and partial (one-way) migrations for 14 individual harriers (Figure 4.1, Table 4.1). Five additional harriers did not migrate and remained in Suisun to breed (Table 4.1). One harrier migrated and bred outside of Suisun the first breeding season and returned and remained in Suisun to breed the following breeding season (ID 23, Table 4.1). A second harrier remained in Suisun as a non-breeder the first breeding season and migrated outside of Suisun to breed the following breeding season (ID 499, Table 4.1). One female harrier migrated south during spring migration to breed on Mendota Wildlife Area (WA; ID 36, Table 4.1). Overall, we identified nest sites across five Western United States (CA, WA, OR, ID, and AK; Table 4.1). Of the 11 breeding areas identified, eight were located on state wildlife areas (Grizzly Island WA, Mendota WA), federal national wildlife refuges (NWR), and a national forest (NF; Table 4.1). The remaining three breeding areas were either remote wilderness areas (Alaska and Idaho), or a rural region consisting primarily of alfalfa and wheat agriculture (Yakima Valley, WA; Table 4.1).

Table 4.1 Transmitter type, date deployed, number of locations, location interval, date of last location, transmitter status, number of complete migrations to and from breeding locations, and name of breeding location for 35 wintering adult female and two adult male Northern Harriers captured in Suisun Marsh, CA across three winter seasons (2017–2018, 2018–2019, and 2019–2020). Status represents last known status of each individual bird (active = transmitter still sending locations and bird alive; inactive = transmitter no longer sending locations and bird is unknown to be alive or deceased; deceased = bird confirmed dead, and transmitter recovered; slipped = transmitter fell off and was recovered and bird likely to still be alive). Breeding locations include general regions or specific locations (NWR = National Wildlife Refuge; NF = National Forest).

ID	**Transmitter Type**	**Date Deployed**	**# Of Locations**	**Location Interval**	**Date of Last Location**	**Status**	**Complete and Partial Migrations**	**Breeding Location(s)**
60	Ecotone	1 Feb 2018	119	2-24 hr	28 Sept 2018	Inactive	None	N/A
61	Ecotone	29 Jan 2018	1,966	1-24 hr	11 Aug 2019	Inactive	1 Spring, 1 Fall	Yakima Valley, WA
65	Ecotone	5 Feb 2018	577	1-3 hr	23 Oct 2018	Inactive	1 Spring	Malheur NWR, OR
66	Ecotone	5 Feb 2018	32	3 hr	8 Feb 2018	Inactive	None	N/A
22	Ecotone	9 Feb 2018	625	3-24 hr	18 May 2020	Inactive	3 Spring, 2 Fall	Malheur NWR, OR
36	Ecotone	22 Jan 2018	1,520	1-24 hr	14 Oct 2018	Inactive	1 Spring, 1 Fall	Mendota NWR, CA
37	Ecotone	5 Feb 2018	3,232	2-12 hr	12 Nov 2019	Inactive	2 Spring, 2 Fall	North Slope, AK
39	Ecotone	6 Feb 2018	160	3-24 hr	7 Feb 2019	Inactive	None	N/A
40	Ecotone	8 Feb 2018	255	3-24 hr	24 July 2018	Deceased	1 Spring	Idaho
41	Ecotone	9 Feb 2018	1,018	3-24 hr	30 Sept 2018	Inactive	1 Spring	Hart Mountain NWR, OR
14	Ecotone	23 Mar 2019	1,152	1-2 hr	7 June 2020	Inactive	None	N/A
19	Ornitela	29 Jan 2019	1,872	0.5-1 hr	21 May 2019	Inactive	1 Spring	Malheur NWR, OR
20	Ornitela	24 Jan 2019	3,901	0.5-2 hr	30 June 2019	Deceased	None	Suisun Marsh, CA
21	Ornitela	24 Jan 2019	124	1 hr	3 Feb 2019	Slipped	None	N/A
23	Ornitela	5 Feb 2019	16,937	0.5-2 hr	22 Feb 2021	Inactive	1 Spring, 1 Fall	Tule Lake NWR & Suisun Marsh, CA
24	Ornitela	5 Feb 2019	1,037	0.5-2 hr	1 April 2019	Inactive	None	N/A

25	Ornitela	11 Feb 2019	1,648	0.5-2 hr	18 May 2019	Inactive	None	N/A
26	Ornitela	18 Feb 2019	13,333	0.5-2 hr	21 Dec 2020	Inactive	None	N/A
27	Ornitela	8 Feb 2019	2,258	0.5-12 hr	3 Sept 2019	Slipped	1 Spring, 1 Fall	Yakima Valley, WA
28	Ornitela	17 Feb 2019	787	0.5-1 hr	29 Mar 2019	Deceased	None	N/A
28.1	Ornitela	31 Mar 2019	1,978	0.5 hr	3 June 2019	Slipped	None	N/A
29	Ornitela	17 Feb 2019	381	0.5-24 hr	8 June 2019	Deceased	None	N/A
30	Ornitela	17 Feb 2019	713	0.5-1 hr	21 Mar 2019	Deceased	None	N/A
30.1	Ornitela	23 Mar 2019	4,331	0.5 hr	14 Aug 2019	Deceased	None	Suisun Marsh, CA
493	Ornitela	16 Dec 2019	5,701	0.5-2 hr	21 Nov 2020	Deceased	None	N/A
494	Ornitela	19 Dec 2019	12,527	0.5 hr	4 May 2021	Inactive	1 Spring, 1 Fall	Southwestern, AK
495	Ornitela	16 Dec 2019	10,752	0.5-1 hr	18 July 2021	Active	None	Suisun Marsh, CA
496	Ornitela	19 Dec 2019	10,848	0.5-2 hr	23 July 2021	Active	2 Spring, 1 Fall	Upper Klamath NWR, OR
497	Ornitela	21 Jan 2020	8,734	0.5 hr	23 July 2021	Active	None	Suisun Marsh, CA
498[*]	Ornitela	23 Dec 2019	6,440	0.5 hr	20 Sept 2020	Inactive	None	East of Suisun Marsh, CA
499	Ornitela	23 Dec 2019	8,504	0.5 hr	26 Feb 2021	Inactive	1 Spring	Upper Klamath NWR, OR
500	Ornitela	30 Dec 2019	2,781	0.5 hr	26 April 2020	Inactive	None	N/A
501	Ornitela	9 Jan 2020	8,378	0.5 hr	16 Nov 2020	Inactive	1 Spring, 1 Fall	Fremont NF, OR
502[*]	Ornitela	28 Jan 2020	126	0.5 hr	3 Feb 2020	Inactive	None	N/A
633	Ornitela	30 Jan 2020	1,624	0.5-1 hr	24 April 2020	Inactive	None	N/A
Total			*136,371*				*18 Spring, 11 Fall*	

[*] Birds 498 and 502 are the only two adult males in our study.

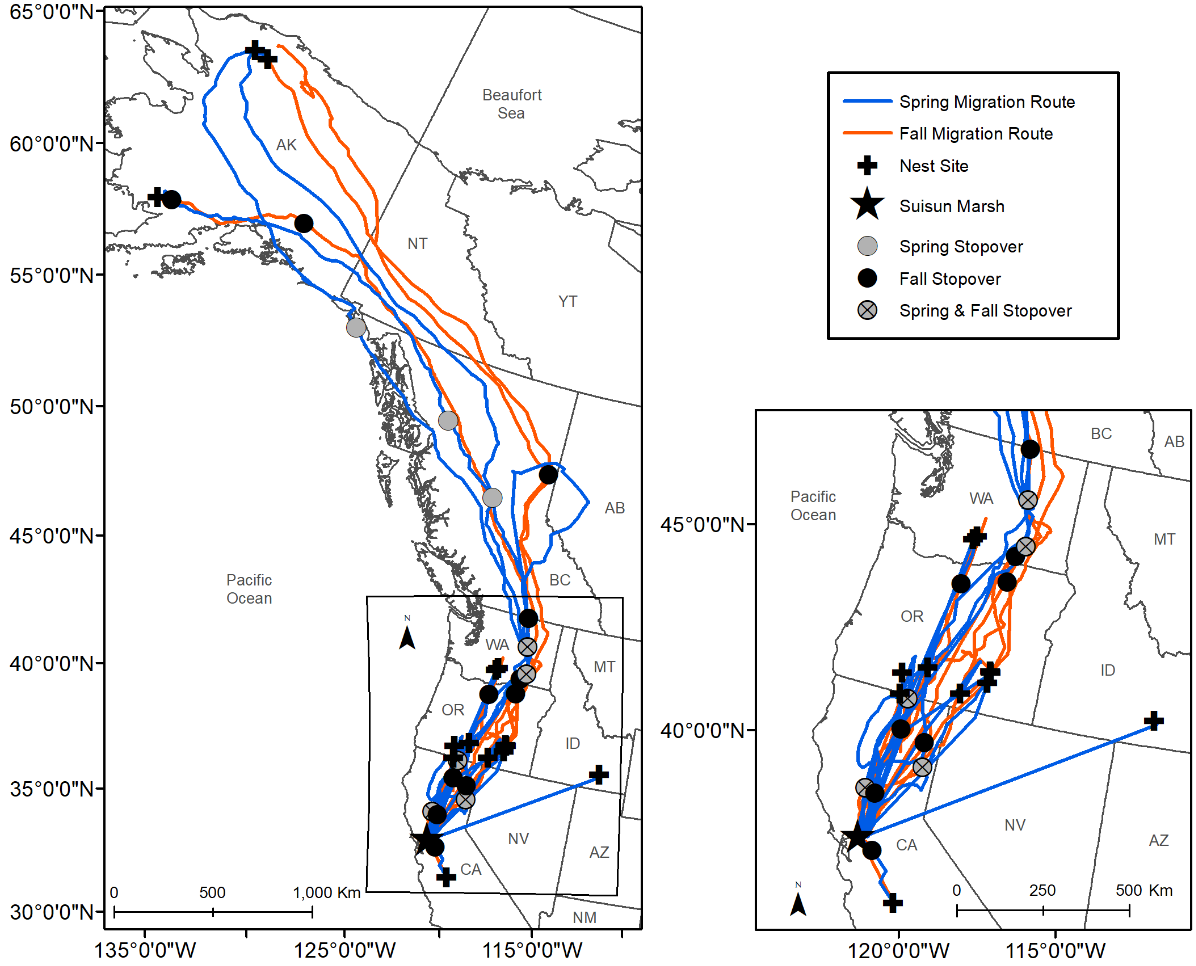

Fig 4.1 Migration maps of 14 adult female Northern Harriers captured on the wintering grounds in Suisun Marsh, CA and breeding across the western North America and an inset map of migration detail. Stopover locations representing both spring and fall stopovers were used by either the same bird during both spring and fall migration, or at least two different birds, but not necessarily during the same stopover (i.e., one bird used this location in the spring while another bird used this location in fall).

Of the 11 returning fall migration birds recorded, 10 harriers returned to Suisun to winter (Table 4.2). One individual returned to Yolo WA (~ 50 km northeast of Suisun), then wintered on Colusa NWR (~100 km north of Suisun), before returning to Suisun at the beginning of the next breeding season to breed (ID 23, Table 4.2). All individuals wintered on Suisun the first winter they were captured and marked with transmitters and all migrant harriers were adult females (Table 4.2).

Table 4.2 Summary of migration dates and locations with mean degrees of latitude and longitude (± SE) for spring and fall migration and stopover areas for wintering adult female Northern Harriers captured in Suisun Marsh across three winter seasons (2017–2018, 2018–2019, and 2019–2020). Stopover locations are > 24 hr stops in migration, except for Bird ID 37 which never had any stopovers > 24 hr. Dashes (-) mean no event occurred in this category. Only breeding migratory individuals are included here. Table format adapted form Linkhart et al 2016.

	Spring Migration				**Breeding**				**Fall Migration**			
		Spring Stopover							**Fall Stopover**			
ID	**Depart Suisun**	**Latitude**	**Longitude**	**Stopover Duration**	**Arrive Breeding**	**Latitude**	**Longitude**	**Depart Breeding**	**Latitude**	**Longitude**	**Stopover Duration**	**Arrive Suisun**
61												
2018	22 Feb	-122.1 ± 0.01	39.4 ± 0.01	22-24 Feb								
		-121.5 ± 0.005	41.9 ± 0.008	25 Feb-5 Mar	8 Mar	-120.6 ± 0.0002	46.4 ± 0.0002	11 Oct	-120.7 ± 0.002	45.1 ± 0.002	12-18 Oct	
									-121.5 ± 0.001	41.9 ± 0.001	23-27 Oct	30 Oct
65												
2018	12 Mar	-121.4 ± 0.001	41.1 ± 0.001	13-15 Mar	17 Mar	-118.8 ± 0.001	43.1 ± 0.004	16 Sept**	-	-	-	-
22												
2018	23 Mar	-	-	-	25 Mar	-118.9 ± 0.003	42.9 ± 0.008	15 Oct	-	-	-	17 Oct
2019	23 Mar**	-	-	-	11 Apr*	-118.9 ± 0.003	42.9 ± 0.008	7 Sept**	-120.4 ± 0.001	40.3 ± 0.001	12-17 Oct	16 Jan**
2020	5 Apr**	-	-	-	14 Apr*	-118.9 ± 0.003	42.9 ± 0.008	18 May**	-	-	-	-
36												
2018	27 Feb	-	-	-	4 Mar	-120.4 ± 0.02	36.7 ± 0.02	2 June	-	-	-	16 June
37												
2018	1 Apr	-118.9 ± 0.01	47.5 ± 0.002	22 Apr-3 May								
		-138.7 ± 0.04	59.2 ± 0.01	10-13 May	23 May	-159.0 ± 0.0001	69.1 ± 0.00003	23 July	-120.6 ± 0.003	55.7 ± 0.004	7-10 Aug	
									-118.6 ± 0.001	46.5 ± 0.001	17 Aug-27 Oct	
									-119.0 ± 0.01	45.5 ± 0.01	28 Oct-2 Nov	22 Nov

2019	18 Apr	-118.8 ± 0.003 -124.1 ± 0.003	46.6 ± 0.001 53.9 ± 0.002	24-27 Apr 3-8 May	21 May	-157.6 ± 0.0005	69.1 ± 0.0002	23 Aug	-118.9 ± 0.001 -121.8 ± 0.005	46.2 ± 0.002 39.3 ± 0.004	5-6 Sept 10-11 Sept	11 Sept
40												
2018	18 Mar[**]	-	-	-	27 Mar[**]	-112.8 ± 0.001	42.7 ± 0.002	-	-	-	-	-
41												
2018	15 Apr	-119.3 ± 0.007	43.4 ± 0.005	16-19 Apr[**]	2 May[**]	-119.8 ± 0.001	42.4 ± 0.001	11 Aug	-120.2 ± 0.001	45.3 ± 0.0003	14 Aug-30 Sept[**]	-
19												
2019	28 Feb	-120.3 ± 0.001	40.3 ± 0.001	1-6 Mar	6 Mar	-118.9 ± 0.0001	43.1 ± 0.0001	20 May[**]	-	-	-	-
23												
2019	30 Apr	-	-	-	1 May	-121.8 ± 0.0003	42.0 ± 0.0003	29 Nov	-121.5 ± 0.001 -122.1 ± 0.0003	41.1 ± 0.001 39.4 ± 0.0006	29 Nov-5 Dec 6-14 Dec	23 Feb[†]
27												
2019	9 Mar[**]	-	-	-	11 Apr[**]	-120.7 ± 0.0001	46.3 ± 0.0001	4 Aug	-120.6 ± 0.0006	40.9 ± 0.0007	7 Aug-11 Aug	13 Aug
494												
2020	19 Apr	-119.0 1 ± 0.0008 -129.2 ± 0.01	47.7 1 ± 0.0005 56.8 1 ± 0.001	23-24 Apr 27-29Apr	5 May	-157.9 ± 0.0002	59.6 ± 0.0001	24 Aug	-156.9 ± 0.004 -119.2 ± 0.001 -119.9 ± 0.001 -121.2 ± 0.0001	59.9 ± 0.002 48.0 ± 0.003 43.4 ± 0.001 42.0 ± 0.0003	25-27 Aug 15-17 Sept 25-30 Sept 2 Oct-20 Nov	23 Nov
496												
2020	21 Mar	-	-	-	23 Mar	-121.9 ± 0.00001	42.5 ± 0.00001	7 Nov	-	-	-	10 Nov
2021	5 Mar	-121.5 ± 0.002	41.9 ± 0.003	6-13 Mar	14 Mar	-121.9 ± 0.0003	42.6 ± 0.0001	-	-	-	-	-
499												
2021	16 Mar				17 Mar	-122.1 ± 0.0001	42.5 ± 0.0002	-	-	-	-	-
501												
2020	30 Mar	-	-	-	2 Apr	-121.1 ± 0.00005	42.8 ± 0.00003	27 Oct	-	-	-	29 Oct

[*] First location at same breeding area from 2018, but not enough locations to determine if nesting was attempted or if this individual was a non-breeder.

[**] First/last date recorded with missing data between this date and departure from/arrival to next location. May not represent true departure/arrival date.

[†] This individual returned to Yolo WA on 15 Dec and then wintered on Colusa NWR from 20 Dec to 20 Feb, then returned to Suisun Marsh on Feb 23 to breed in 2020.

We report all migration distances, durations, and speeds below as the "mean (± standard error)" unless otherwise noted. Mean spring migration distance was 2219.8 km (± 806.1 km) and mean fall migration distance was 2859.1 km (± 1103.4 km) for a mean total round-trip migration distance of 6231.1 km (± 2545.8 km; Table 4.3). We recorded the three longest-distance round-trip migrations for any Northern Harrier with one individual (ID 37) migrating a total of 19472.2 km and 13319.2 km across two years, and a second individual (ID 494) migrating a total of 15780.9 km (Table 4.3). Both individuals were adult females that bred in Alaska and returned to Suisun to winter.

Fall migration lasted more than twice as long as spring migration, on average (fall = 30.2 ± 12.8 d, spring = 12.2 ± 4.2 d), and mean total migration duration was 47.4 d (± 19 d, Table 4.3). Fall stopovers lasted more than three times longer than spring stopovers, on average (fall = 24.6 ± 11.7 d, spring = 7.0 ± 1.6 d), with a mean total stopover duration of 46.0 d (± 19.2 d, Table 4.3). Taken together, mean spring stopover duration was nearly 60% of the mean total spring migration duration, and mean fall stopover duration was > 80% of the mean fall total migration duration (Table 4.3). Spring stopovers were located at seven different general locations, four of which occurred on state wildlife areas (Honey Lake WA) and federal national wildlife refuges (Tule Lake NWR, Sacramento NWR, Upper Klamath NWR), and the remaining locations were on remote wilderness or rural agricultural areas in WA, BC, and coastal AK (Figure 4.1). There were 12 different locations identified for fall stopovers, with several overlapping spring stopover locations (Figure 4.1). Six locations occurred on state wildlife areas (Honey Lake WA, Gray Lodge WA) and federal national wildlife refuges (Tule Lake NWR, Sacramento NWR, McNary NWR), and the remaining locations were on remote wilderness or rural agricultural areas across CA, WA, OR, BC, and AK (Figure 4.1). Three birds used at least one of the same stopover locations during both spring and fall migration, and seven birds used at least one of the same stopover locations as at least one other bird (Figure 4.1).

Spring migration speed tended to be slightly faster (192.5 ± 28.9 km d^{-1}) than fall migration speed (131.1 ± 32.3 km d^{-1}; Table 4.3). Median spring departure date was 22 March (day of year 81), and median spring arrival date (arrival to breeding area) was just three days later on 25 March (day of year 84). Median fall departure date was 25 August (day of year 237) with a much longer migration resulting in a median fall arrival date (arrival to wintering area) of 30 October (day of year 303; Figure 4.2). Overall, spring migration was shorter in both distance and days, with fewer and shorter stopovers, and a slightly faster migration speed compared to fall migration.

We categorized six harriers as long-distance migrants and eight as short-distance migrants based on median migration distance traveled during spring migration (667.2 km, Table 3). One individual that travelled 703.2 km was considered a short-distance migrant because her breeding location was the same as other short-distance migrants in this study regardless of the slightly longer total distance travelled during spring migration (ID 65, Table 4.3). The null hypothesis was the top model for all stage-1 analyses testing for differences between migration distance, stopover duration, migration speed, arrival time, and departure time between long- and short-distance migrants. Hence short- and long-distance migrants showed no statistically supported differences in these migration descriptors.

Table 4.3 Summary of migration strategy (short- or long-distant migrant), migration distance (km), duration (migration d), and speed (km d^{-1}) for complete spring and fall migrations for 14 wintering adult female Northern Harriers captured in Suisun Marsh, CA across three winter seasons (2017–2018, 2018–2019, and 2019–2020). Migration distances, durations, and rates include from the date birds left a wintering/breeding area to the first day they arrived at a breeding/wintering area, including distance and dates traveled during stopovers. Dashes (-) mean no/not enough locations were recorded in this category. Only breeding migratory individuals are included here.

			Migration Distance					Migration Duration					Stopover Duration					Migration Speed			
ID	**Year**	**Strategy**	**Spring**	**Fall**	**Total**	**Mean**	**SE**	**Spring**	**Fall**	**Total**	**Mean**	**SE**	**Spring**	**Fall**	**Total**	**Mean**	**SE**	**Spring**	**Fall**	**Mean**	**SE**
61	2018	Long	993.9	1035.7	2029.6	1014.8	20.9	15	20	35	17.5	2.5	10	10	20	10	0	66.3	51.8	59.0	7.2
65	2018	Short[*]	703.2	-	-	-	-	6	-	-	-	-	2	-	-	-	-	117.2	-	-	-
22	2018	Short	631.2	835.5	1466.7	733.3	102.1	3	3	6	3	0	-	5	-	-	-	210.4	278.5	244.5	34.1
36	2018	Short	233.5	430.6	644.2	332.1	98.6	6	15	21	10.5	4.5	-	-	-	-	-	38.9	28.7	33.8	5.1
37	2018	Long	11210.4	8261.8	19472.2	9736.1	1474.3	53	119	172	86	33	14	79	93	46.5	32.5	211.5	69.4	140.5	71.1
37	2019	Long	6802.2	6517.0	13319.2	6659.6	142.6	34	20	54	27	7	8	2	10	5.0	3.0	200.1	325.9	263.0	62.9
40	2018	Short	551.0[**]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
41	2018	Long	923.8[**]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	2019	Long	1275.2	-	-	-	-	7	-	-	-	-	5	-	-	-	-	182.2	-	-	-
23	2019	Short	499.2	612.3	1111.5	555.7	56.5	2	17	19	9.5	7.5	-	14	-	-	-	249.6	36.0	142.8	106.8
27	2019	Long	927.2[**]	1056.2	-	-	-	-	10	-	-	-	-	4	-	-	-	-	105.6	-	-
494	2020	Long	7032.1	8748.8	15780.9	7890.5	858.3	17	91	108	54	37	3	58	61	30.5	27.5	413.7	96.1	254.9	158.8
496	2020	Short	554.0	545.9	1099.9	539.9	4.1	3	4	7	3.5	0.5	-	-	-	-	-	184.7	136.5	160.6	24.1
496	2021	Short	621.2	-	-	-	-	9	-	-	-	-	7	-	-	-	-	69.0	-	-	-
499	2021	Short	510.6	-	-	-	-	2	-	-	-	-	-	-	-	-	-	255.3	-	-	-
501	2020	Short	608.5	547.2	1155.7	577.9	30.7	2	3	5	2.5	0.5	-	-	-	-	-	304.3	182.4	243.3	60.9
		Mean	*2129.8*	*2859.1*	*6231.1*	-	-	*12.2*	*30.2*	*47.4*	-	-	*7.0*	*24.6*	*46.0*	-	-	*192.5*	*131.1*	-	-
		SE	*806.1*	*1103.4*	*2545.8*	-	-	*4.2*	*12.8*	*19.0*	-	-	*1.6*	*11.7*	*19.2*	-	-	*28.9*	*32.3*	-	-
		Median	*667.2*	*935.6*	*1466.7*	-	-	*6.0*	*16.0*	*21.0*	-	-	*7.0*	*10.0*	*40.5*	-	-	*200.1*	*100.9*	-	-

[*] This individual is considered a short-distance migrant because her breeding location was the same as other short-distance migrants, despite traveling farther than the median spring migration distance.

[**] Migration distance represents straight line distance from last date in Suisun to first date on breeding area. Missing dates for full migration. Cannot calculate accurate duration or rate of travel.

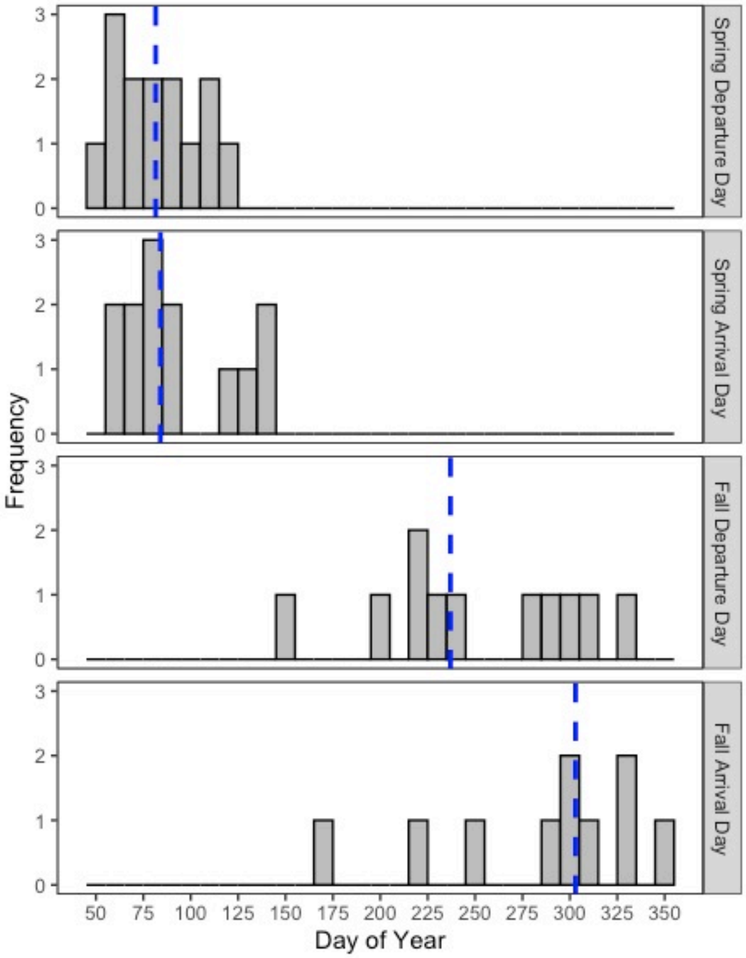

Figure 4.2 Histograms of spring (A-B) and fall (C-D) departure and arrival dates for wintering adult female Northern Harriers captured in Suisun Marsh, CA (2017-2019). Dotted blue vertical line represents median day of year.

3.3 Home Range Estimation and Habitat Selection

We report all home range sizes, habitat proportions, and selection ratios below based on 95% KDE home ranges as “mean/estimate (± standard error)” unless otherwise noted. The 95% KDE home range size for nest sites was very similar across all 14 adult female harriers with a mean home range size of 0.33 km^2 (± 0.17 km^2) and a median home range size of 0.14 km^2 (Table 4.4). High proportions of wetland (0.98 ± 0.007) and shrub habitat (0.58 ± 0.19) were used at nest sites, and the use of these habitat types was higher than their availability within home ranges (Table 4.4). Cultivated habitat had a high proportion of use relative to availability, as well, but only two individuals selected nest sites in this habitat type (Table 4.4). Overall habitat selection was significantly different than available habitat across all nest sites (χ^2 = 13260.6, df = 9, $p < 0.001$, $n = 14$). Based on Manly selection ratios, only wetland habitat was strongly selected for at nest sites ($Wi = 1.08 \pm 0.005$), though shrub ($Wi = 0.97 \pm 0.04$) and cultivated ($Wi = 0.98 \pm 0.04$) habitat showed weak selection with confidence intervals overlapping one (Figure 4.3 A). Grassland habitat was generally selected against ($Wi = 0.60 \pm 0.3$), but variation in this selection was high, with all other habitat types not selected (Figure 4.3 A).

Table 4.4 Summary of nest site kernel density estimator (KDE) home range sizes (km^2) and proportion of available (total count of all grid cells for each habitat type/total number of cells) and used (total count of each habitat type at each point location/total used point locations) habitat types within each 95% home range for 14 migratory breeding female Northern Harriers from 2016 NLCD layers for the continental United States and Alaska. Other contains barren and developed land (open space, and low, medium, and high intensity). Dashes (-) mean no habitat was available or used in this category.

		KDE Home Range			**Available Habitat**							**Used Habitat**						
ID	**Year**	**99%**	**95%**	**50%**	**Wetland**	**Shrub**	**Cultivated**	**Forest**	**Grassland**	**Open Water**	**Other**	**Wetland**	**Shrub**	**Cultivated**	**Forest**	**Grassland**	**Open Water**	**Other**
61	2018	0.17	0.11	0.02	-	-	1.00	-	-	-	-	-	-	1.00	-	-	-	-
65	2018	0.22	0.12	0.02	0.80	0.01	-	-	0.19	-	-	0.97	-	-	-	0.03	-	-
22	2018	0.93	0.59	0.05	1.00	0.001	-	-	-	-	-	1.00	-	-	-	-	-	-
36	2018	0.09	0.06	0.004	0.99	-	0.02	-	-	-	-	1.00	-	-	-	-	-	-
37	2018	0.02	0.01	0.001	-	1.00	-	-	-	-	-	-	1.00	-	-	-	-	-
37	2019	4.97	2.83	0.13	0.001	0.94	-	-	0.06	0.002	-	-	0.92	-	-	0.08	-	-
40	2018	0.01	0.006	0.0007	-	1.00	-	-	-	-	-	-	1.00	-	-	-	-	-
41	2018	0.43	0.15	0.01	0.69	0.12	-	0.19	-	-	-	0.96	0.04	-	0.002	-	-	-
19	2019	0.24	0.16	0.02	0.91	0.09	-	-	-	-	-	0.96	0.04	-	-	-	-	-
23	2019	0.13	0.03	0.001	1.00	-	-	-	-	-	-	1.00	-	-	-	-	-	-
27	2019	0.37	0.21	0.03	-	0.04	0.80	-	0.01	-	0.16	-	-	0.94	-	-	-	0.06
494	2020	0.13	0.02	0.001	-	1.00	-	-	-	-	-	-	1.00	-	-	-	-	-
496	2020	0.04	0.02	0.001	0.67	0.33	-	-	-	-	-	0.94	0.06	-	-	-	-	-
496	2021	0.33	0.20	0.02	0.99	-	-	-	-	0.01	-	1.00	-	-	-	-	0.003	-
499	2021	1.19	0.39	0.04	1.00	-	-	-	-	-	-	1.00	-	-	-	-	-	-
501	2020	1.52	0.36	0.02	0.92	0.00	-	-	-	0.08	-	1.00	-	-	-	-	0.002	-
	Mean	*0.67*	*0.33*	*0.02*	*0.81*	*0.41*	*0.60*	*0.19*	*0.09*	*0.03*	*0.16*	*0.98*	*0.58*	*0.97*	*0.002*	*0.05*	*0.003*	*0.06*
	SE	*0.31*	*0.17*	*0.01*	*0.09*	*0.15*	*0.30*	-	*0.05*	*0.02*	-	*0.01*	*0.19*	*0.03*	-	*0.02*	*0.001*	-
	Median	*0.23*	*0.14*	*0.02*	*0.92*	*0.12*	*0.80*	*0.19*	*0.06*	*0.01*	*0.16*	*1.00*	*0.92*	*0.97*	*0.002*	*0.05*	*0.003*	*0.06*

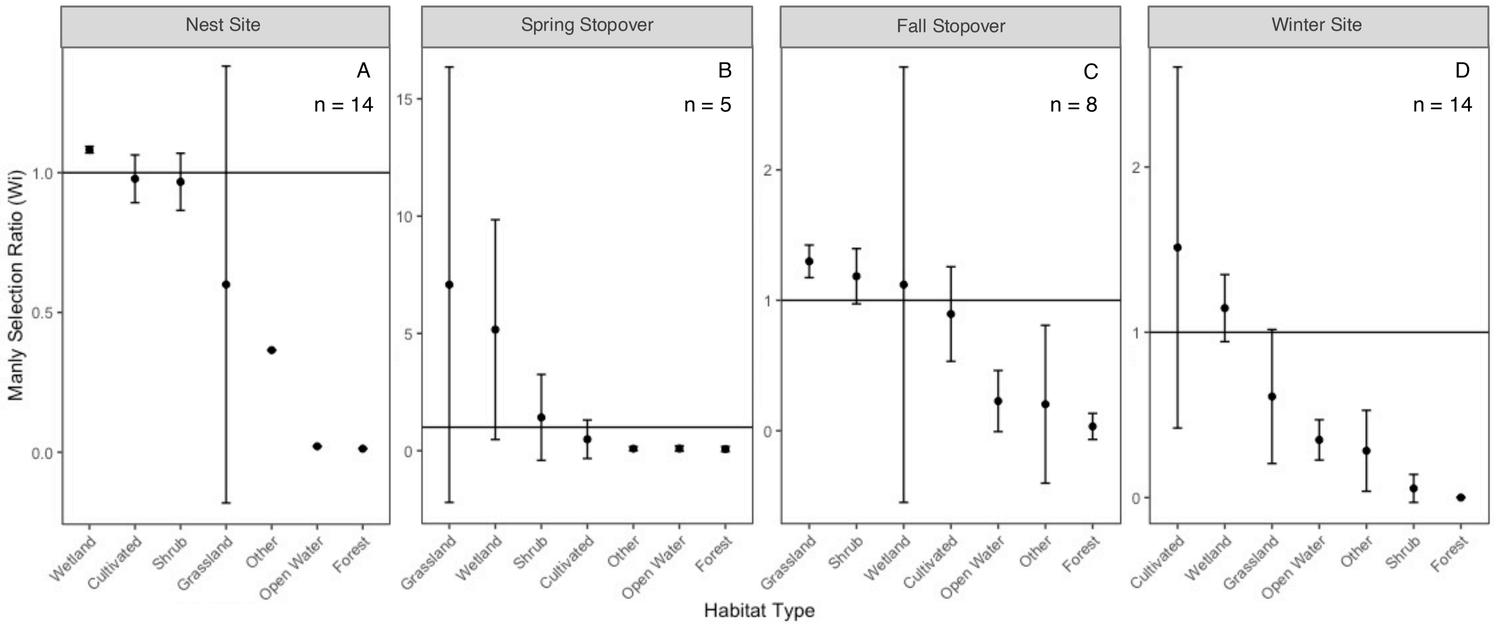

Figure 4.3 Global Manly selection ratios (*Wi* ± 95% CI) for each habitat type within 95% kernel density estimator home ranges for A) nest sites, B) spring stopover sites, C) fall stopover sites, and D) winter sites for adult female Northern Harriers captured in Suisun Marsh, CA (2018–2020). Note the x-axis is ordered differently on each graph (from highest to lowest selection ratio). The horizontal black line at 1.0 Wi represents the threshold for positive and negative selection. Selection ratios above 1.0 indicate positive selection (preference) whereas selection ratios below 1.0 indicate negative selection (avoidance).

There were only five females across 10 spring stopovers that had enough locations to calculate KDE home ranges (Table 4.5). The 95% KDE home range sizes varied considerably, with a mean home range size of 265.7 km^2 (± 162.9 km^2) and a median home range size of 97.3 km^2 (Table 4.5). Wetland (0.62 ± 0.18), shrub (0.30 ± 0.07), cultivated (0.40 ± 0.19), and grassland habitats (0.27 ± 0.09) were proportionately the most used, with only wetland and grassland habitat being used considerably more than available habitat (Table 4.5). Forest and open water habitat were both ≤ 20% of habitat used and likely represent flyover locations (Table 4.5). Overall habitat selection was significantly different from available habitat ($\chi^2 = 4950.7$, df = 16, $p < 0.001$, $n = 5$). There was a strong positive selection for grassland ($Wi = 7.1 \pm 3.8$) and wetland habitat ($Wi = 5.2 \pm 1.9$), though confidence intervals were large and overlapped one (Figure 4.3 B). There was also a positive selection for shrub habitat ($Wi = 1.4 \pm 0.7$) but confidence intervals also overlapped one and all other habitat types were not selected (Figure 4. 3 B).

Table 4.5. Summary of spring stopover kernel density estimator (KDE) home range sizes (km^2) and proportion of available (total count of all grid cells for each habitat type/total number of cells) and used (total count of each habitat type at each point location/total used point locations) habitat types within each 95% home range for six migratory female Northern Harriers from 2016 NLCD layers for the continental United States and Alaska, and 2015 NALCMS layer for Canada. Some stopovers did not have enough locations to generate home ranges (at least five locations needed). Other contains barren land, developed land (open space, and low, medium, and high intensity developed), and perennial ice and snow. Dashes (-) mean no habitat was available or used in this category.

			KDE Home Range			**Available Habitat**							**Used Habitat**						
ID	**Year**	**Stopover**	**99%**	**95%**	**50%**	**Wetland**	**Shrub**	**Cultivated**	**Forest**	**Grassland**	**Open Water**	**Other**	**Wetland**	**Shrub**	**Cultivated**	**Forest**	**Grassland**	**Open Water**	**Other**
61	2018	1	97.2	64.8	13.0	0.38	-	0.59	-	-	0.01	0.02	1.00	-	-	-	-	-	-
		2	194.8	139.7	38.1	0.06	0.04	0.61	0.001	0.01	0.26	0.03	0.27	-	0.70	-	-	0.03	-
37	2018	1	566.2	387.4	59.6	0.003	0.47	0.34	-	0.17	0.001	0.03	-	0.41	0.18	-	0.40	-	0.01
		2	2429.8	1696.3	412.6	0.02	0.09	-	0.41	0.00	0.41	0.07	0.14	0.14	-	0.21	0.14	0.07	0.29
	2019	1	19.0	13.2	3.5	0.33	0.50	-	0.14	-	0.03	0.33	-	0.50	0.05	-	0.45	-	-
		2	222.2	148.1	24.7	0.001	0.27	-	0.46	0.02	0.21	0.04	-	0.41	-	0.15	-	0.44	-
19	2019	1	18.6	13.0	2.3	0.37	0.35	0.22	-	0.03	-	0.03	0.74	0.18	0.08	-	-	-	0.01
494	2020	1	1.7	1.1	0.2	-	0.06	0.83	-	0.06	-	0.05	-	-	1.00	-	-	-	-
		2	190.0	129.7	31.3	-	0.17	-	0.58	0.04	0.004	0.20	-	0.44	-	0.25	0.07	0.25	-
496	2021	1	99.0	63.8	10.4	0.11	0.16	0.44	0.00	0.02	0.27	0.01	0.94	0.06	-	-	-	-	-
		Mean	*383.9*	*265.7*	*59.6*	*0.16*	*0.24*	*0.50*	*0.27*	*0.04*	*0.15*	*0.08*	*0.62*	*0.30*	*0.40*	*0.20*	*0.27*	*0.20*	*0.10*
		SE	*233.2*	*162.9*	*39.7*	*0.06*	*0.06*	*0.09*	*0.10*	*0.02*	*0.06*	*0.03*	*0.18*	*0.07*	*0.19*	*0.03*	*0.10*	*0.09*	*0.09*
		Median	*144.5*	*97.3*	*18.9*	*0.08*	*0.17*	*0.52*	*0.28*	*0.03*	*0.12*	*0.04*	*0.74*	*0.41*	*0.18*	*0.21*	*0.27*	*0.16*	*0.01*

There were eight females across 17 fall stopovers with enough locations to calculate KDE home ranges (Table 4.6). The 95% KDE home ranges were small compared to spring stopovers, with a mean home range size of 67.1 km^2 (± 22.2 km^2) and median home range size of 14.1 km^2 (Table 4.6). Like spring stopovers, habitat use also varied greatly with > 30% use each for wetland, shrub, cultivated, and grassland habitat (Table 4.6). Also like spring stopovers, only wetland and grassland habitat were used considerably more than available habitat (Table 4.6). Overall habitat selection was significantly different than available habitat ($\chi^2 = 1182.5$, df = 24, $p < 0.001$, $n = 8$). There was a strong positive selection for grassland habitat ($Wi = 1.3 \pm 0.05$), and a positive selection for shrub habitat ($Wi = 1.2 \pm 0.09$), though confidence intervals overlapped one for shrub habitat (Figure 4.3 C). There was also a positive selection for wetland habitat, though this selection showed considerable variation (Figure 4.3 C). All other habitat types were not selected (Figure 4. 3C).

Table 4.6. Summary of fall stopover kernel density estimator (KDE) home range sizes (km^2) and proportion of available (total count of all grid cells for each habitat type/total number of cells) and used (total count of each habitat type at each point location/total used point locations) habitat types within each 95% home range for eight migratory female Northern Harriers from 2016 NLCD layers for the continental United States and Alaska, and 2015 NALCMS layer for Canada. Some stopovers did not have enough locations to generate home ranges (at least five locations needed). Other contains barren land, developed land (open space, and low, medium, and high intensity developed), and perennial ice and snow. Dashes (-) mean no habitat was available or used in this category.

			KDE Home Range			**Available Habitat**							**Used Habitat**						
ID	**Year**	**Stopover**	**99%**	**95%**	**50%**	**Wetland**	**Shrub**	**Cultivated**	**Forest**	**Grassland**	**Open Water**	**Other**	**Wetland**	**Shrub**	**Cultivated**	**Forest**	**Grassland**	**Open Water**	**Other**
61	2018	1	7.2	5.1	1.4	0.28	0.38	-	0.33	0.001	0.01	0.28	-	0.47	0.15	-	0.38	-	-
		2	4.6	3.2	0.7	0.45	-	0.31	-	0.004	0.24	0.001	0.93	-	-	-	-	0.07	-
22	2019	1	2.1	1.5	0.4	0.37	0.56	0.02	0.002	0.02	0.04	0.001	0.86	0.14	-	-	-	-	-
36	2018	1	12.9	7.4	0.9	-	-	0.99	-	-	-	0.02	-	-	1.00	-	-	-	-
37	2018	1	58.0	40.2	9.1	0.001	0.16	0.59	0.21	0.003	0.003	0.03	-	-	1.00	-	-	-	-
		2	69.1	38.4	7.7	-	0.35	0.15	-	0.38	0.10	0.02	-	0.25	0.01	-	0.74	-	-
		3	756.9	517.2	113.5	0.01	0.20	0.16	0.001	0.62	-	0.02	-	0.17	0.27	-	0.56	-	-
	2019	1	5.7	3.9	1.0	0.17	0.20	0.36	0.002	0.004	0.25	0.01	0.22	0.22	0.22	-	-	0.33	-
		2	45.9	32.0	7.2	0.32	-	0.65	-	0.001	0.01	0.03	0.38	-	0.50	-	-	0.13	-
41	2018	1	14.9	9.2	0.8	-	0.24	0.52	-	0.21	-	0.04	-	0.07	0.76	-	0.04	-	0.13
23	2019	2	10.8	7.3	1.5	0.09	0.00	0.26	0.04	0.11	0.47	0.02	0.47	-	0.18	-	0.08	0.27	-
		3	3.9	2.1	0.3	0.95	-	0.03	-	-	0.004	0.02	1.00	-	-	-	-	-	-
27	2019	1	14.1	8.6	1.1	0.02	0.15	0.58	-	0.20	0.05	-	0.04	0.04	0.85	-	0.07	-	-
494	2020	1	73.4	49.5	6.0	0.02	0.87	-	0.004	0.05	0.06	-	-	0.98	-	-	0.02	-	-
		2	51.7	34.7	8.1	0.08	0.08	-	0.65	-	0.20	-	0.10	-	-	0.25	-	0.65	-
		3	36.4	26.9	6.3	0.00	0.84	0.07	0.004	0.06	-	0.03	-	0.88	0.02	-	0.10	-	-
		4	8.7	3.2	0.3	0.02	0.47	0.07	0.001	0.41	0.01	0.02	-	0.19	0.06	-	0.74	-	0.02
		Mean	*99.8*	*67.1*	*13.1*	0.20	0.35	0.34	0.13	0.15	0.11	0.04	0.50	0.34	0.42	0.25	0.30	0.29	0.07
		SE	*32.4*	*22.2*	*4.7*	0.07	0.08	0.08	0.07	0.05	0.04	0.02	0.14	0.11	0.11	-	0.10	0.10	0.06
		Median	*21.3*	*14.1*	*2.8*	0.08	0.24	0.29	0.004	0.05	0.05	0.02	0.42	0.20	0.25	0.25	0.10	0.27	0.07

Lastly, we calculated wintering home range sizes for 14 adult female harriers across 21 total winter seasons. There was high variation in 95% KDE home range sizes with a mean size of 177.4 km^2 (± 84.6 km^2) but a median size of only 20.0 km^2 (Table 4.7). Despite home range size, habitat use within home ranges was strongly associated with wetland and cultivated habitat. Mean proportion of wetland and cultivated habitat used was 0.74 (± 0.07) and 0.40 (± 0.11), and was slightly higher than available habitat, with 0.60 (± 0.06) and 0.21 (± 0.08) wetland and cultivated habitat available, respectively (Table 4.7). Based on Manly selection ratios wetland ($Wi = 1.15 \pm 0.08$) and cultivated habitat ($Wi = 1.51 \pm 0.44$) were the two most selected habitat types, though their confidence intervals overlapped one indicating variation in selection (Figure 4.3 D). All other habitat types were not selected (Figure 4.3 D). Overall habitat selection was significantly different than available habitat ($\chi^2 = 1962.75$, df = 35, $p < 0.001$, $n = 14$).

The null hypothesis was the top model for all but one stage-1 analyses testing for differences between home range sizes and habitat use between long- and short-distance migrants. Only wetland habitat use at nest sites was selected as a top model ($K = 1$, *-2 loglikelihood* = -4.7, AICc = 17.5, ΔAICc = 0.00, $\omega_i = 0.60$) with short-distance migrants using significantly more wetland habitat for nest sites than long-distance migrants ($\beta = -14.0$, SE = 7.2, z-value = -1.9, $p = 0.05$; Figure 4.4).

Table 4.7. Summary of wintering kernel density estimator (KDE) home range sizes (km^2) and proportion of available habitat types within each 95% home range for 14 wintering female Northern Harriers in Suisun Marsh, CA from 2016 NLCD layers for the continental United States and Alaska. Other contains barren and developed land (open space, and low, medium, and high intensity). Only complete winter seasons are included here. Dashes (-) mean no habitat was available or used in this category.

		KDE Home Range			Available Habitat								Used Habitat						
ID	Year	99%	95%	50%	Wetland	Shrub	Cultivated	Forest	Grassland	Open Water	Other		Wetland	Shrub	Cultivated	Forest	Grassland	Open Water	Other
61	2018	4.1	2.5	0.4	0.95	-	-	-	0.01	0.03	0.01	0.00	0.99	-	-	-	-	0.01	-
	2019	36.5	18.9	2.0	0.85	-	0.02	-	0.05	0.07	0.02	0.00	0.98	-	-	-	0.01	0.01	-
65	2018	102.6	68.0	12.4	0.70	-	0.01	-	0.02	0.27	0.01	0.00	0.94	-	-	-	-	0.05	0.01
22	2018	9.7	6.4	1.1	0.88	-	0.001	-	0.003	0.12	0.002	0.00	0.97	-	-	-	-	0.03	-
36	2018	39.1	20.0	2.0	0.76	-	-	-	0.001	0.23	0.01	0.00	0.99	-	-	-	-	0.01	0.01
	2019	188.6	116.4	16.0	0.48	0.002	0.13	-	0.04	0.31	0.04	0.00	0.81	-	0.17	-	-	0.03	-
37	2018	1631.1	1127.0	252.1	0.20	0.03	0.39	0.001	0.15	0.18	0.06	0.00	0.45	-	0.13	-	0.25	0.12	0.05
	2019	603.7	306.6	28.7	0.16	0.01	0.55	-	0.08	0.17	0.04	0.00	0.07	-	0.37	-	0.47	0.07	0.02
	2020	2291.1	1486.1	247.7	0.03	0.004	0.76	-	0.06	0.10	0.04	0.00	0.08	-	0.85	-	0.01	0.05	0.01
40	2018	123.4	87.9	17.0	0.58	0.01	0.01	-	0.11	0.29	0.01	0.00	0.78	-	-	-	-	0.22	-
41	2018	15.5	10.5	2.7	0.91	-	0.001	-	0.01	0.08	0.00	0.00	0.97	-	-	-	-	0.03	-
19	2019	17.4	10.3	1.0	0.86	-	-	-	0.002	0.12	0.02	0.00	0.98	-	-	-	-	0.02	0.003
23	2019	551.5	237.3	19.2	0.13	0.01	0.57	-	0.07	0.18	0.03	0.00	0.05	0.001	0.87	-	0.03	0.03	0.02
	2020	79.3	54.9	12.2	0.13	-	0.83	-	0.001	0.01	0.03	0.00	0.50	-	0.50	-	-	0.00	0.004
27	2019	26.4	18.8	3.0	0.73	-	0.003	-	0.04	0.20	0.02	0.00	0.92	-	0.01	-	-	0.07	-
494	2020	8.6	4.6	0.3	0.59	-	0.001	-	0.05	0.34	0.02	0.00	0.78	-	-	-	0.02	0.19	0.01
	2021	28.2	13.7	1.1	0.77	-	-	-	0.000	0.23	0.002	0.00	0.98	-	-	-	-	0.02	-
496	2020	171.0	79.5	8.0	0.68	0.004	0.01	-	0.09	0.21	0.01	0.00	0.87	-	-	-	0.001	0.13	-
	2021	74.1	32.1	3.7	0.79	0.01	0.002	-	0.04	0.15	0.01	0.00	0.94	-	-	-	-	0.06	-
499	2021	17.5	11.7	1.9	0.80	-	-	-	0.002	0.19	0.01	0.00	0.91	-	-	-	0.003	0.09	0.002
501	2020	18.3	12.4	0.7	0.70	-	0.03	-	0.12	0.13	0.02	0.00	0.54	-	0.31	-	0.10	0.05	0.001
	Mean	*287.5*	*177.4*	*30.2*	0.60	0.01	0.21	0.001	0.05	0.17	0.02	0.00	0.74	0.001	0.40	-	0.10	0.06	0.012
	SE	*128.6*	*84.6*	*16.0*	0.06	0.003	0.08	-	0.01	0.02	0.003	0.00	0.07	-	0.11	-	0.05	0.01	0.00
	Median	*39.1*	*20.0*	*3.0*	0.70	0.01	0.01	0.001	0.04	0.18	0.02	0.00	0.91	0.001	0.34	-	0.02	0.05	0.01

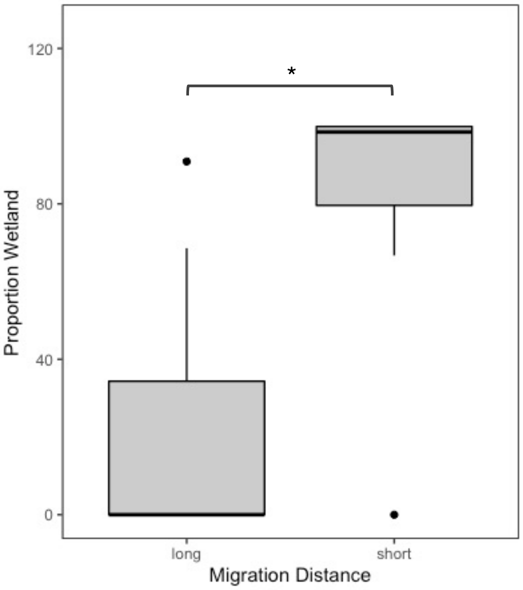

Figure 4.4. Boxplots of proportion wetland habitat in 95% KDE nest site home range for long and short distance migrant adult female Northern Harriers captured in Suisun Marsh, CA (2017-2019). Asterisk represents a significant difference between long- and short-distance migrants (p = 0.05).

4. Discussion

Our study is the first to describe detailed migration ecology and habitat selection of Northern Harriers in North America using fine-scale location data collected from lightweight solar GPS/GSM transmitters. We discovered a diverse breeding range in our study population, with harriers breeding from central California to as far north as the North Slope of Alaska. Despite this large range, our results suggest harriers exhibit strong site fidelity for Suisun March as a wintering area each year. These results highlight the importance of Suisun for not only sustaining the local resident breeding population (Chapters 1 and 2), but also providing a crucial wintering area for harriers from wide-ranging breeding populations across Western North America.

We also determined that harriers wintering in Suisun are primarily migratory, with some individuals remaining in Suisun as either non-breeding or breeding individuals. Overall, harriers that bred in more than one year displayed strong site fidelity for the same breeding areas. Further, harriers captured during the breeding season in Suisun have been found to be year-round residents (Chapter 1). Taken together, these results suggest two populations coexist in Suisun, with the wintering harrier population exhibiting partial migration (called "breeding partial migration", Chapman et al. 2011). Suisun is located at a latitude where winters are neither too harsh nor too mild, which is a primary predictor of partial migration (Lundberg 1988), though several alternative hypotheses exist today (Chapman et al. 2011) and are beyond the scope of this study. Nonetheless, migratory females in this study all bred in locations where harsh winter weather exists (i.e., snowfall, freezing ambient temperatures), which could influence winter survival should they not migrate to more southerly latitude wintering grounds.

We also recorded the three longest-distance migrations for any Northern Harriers to date across two individuals breeding in Alaska, ranging from 13,000 to nearly 20,000 km traveled roundtrip. Before this study, harriers that migrated > 1,500 km were considered long-distance migrants, but no precise migration distances had been documented (Smith et al. 2020). In this study, mean total migration distance was > 6,000 km, and with birds we considered long-distance in our study excluded, the mean total migration distance was ~ 1,100 km, which is consistent with the accepted definition of long- versus short-distance migrants. Harriers are infrequently observed at most migration monitoring stations, comprising 1-4% of observations across North America (Binford 1979, Titus and Fuller 1990, Smith et al. 2020). However, they are the most common species observed during spring migration in interior Alaska (Swem 1982, Mindell and Mindell 1984, McIntyre and Ambrose 1999). At least two individuals not included in this study were migrating through British Columbia in a seemingly northwesterly trajectory before transmitter failure, suggesting Alaska was their breeding destination. One additional individual not included in this study migrated to west-central Alaska, but breeding could not be confirmed before transmitter failure. These six harriers provide strong evidence that the winter origin of at least part of the Alaskan breeding population are migrants from the Pacific Flyway, and more specifically, overwinter in Suisun Marsh.

Long-distance migrants face different challenges than short-distance migrants, and as a result may require different management actions. For example, seasonal differences in long-distance migration routes can influence metapopulation structure, thereby affecting dispersal, recruitment, and overall population trends (Szczys et al. 2017). Determining migratory corridors, stopover locations, and breeding locations for metapopulations is the first step in developing focused conservation actions that could influence range-wide population stability or growth. More research is needed into the breeding populations of migratory harriers in our study to better understand where populations may be facing the biggest threats for decline (Szczys et al. 2017). In addition to breeding location threats, winter locations are where birds prepare for migration and can influence reproductive success the following breeding season. These carry-over effects have been well-documented in migratory birds, with various metrics of body condition and reproductive potential on the breeding grounds influenced by overwintering conditions (e.g., Marra et al. 1998, Norris and Marra 2007, Briedis et al. 2018, Laursen et al. 2019a, b). Ensuring Suisun Marsh is managed so that it provides high-quality suitable habitat and healthy prey populations year-round is one action that will undoubtedly benefit harriers across populations.

Migration timing is not well documented in Western North America, so comparisons with other observations are limited. In our population, spring departure from Suisun ranged from late-February to late-May, which is generally consistent with spring migration timing and passage dates in other regions of North America (Goodrich and Smith 2008, Smith et al. 2020). The median arrival date to breeding areas was just three days after median departure date, and spring stopovers were very short (7 days on average) or non-existent with many harriers stopping only at sunset and continuing migration at sunrise the next morning, suggesting little to no stopping for refueling. Further, the mean speed of spring migration was nearly 200 km d^{-1}, which is comparable to migration speeds reported for other raptor species (e.g., Fuller et al. 1998, Kjellén et al. 2001). Thus, spring migration is short and fast and suggests strong selection pressure to reach the breeding grounds early to secure a mate, territory, and increase reproductive success (McNamara et al. 1998, Kokko 1999). Fall migration timing is consistent with timing documented at migration monitoring stations across North America, with a protracted fall migration spanning nearly three months (Goodrich and Smith 2008, Smith et al. 2020). In our study, fall migration had considerably more and longer stopovers (~ 25 days on average), and migration speed was much slower than spring migration, with birds covering ~ 60 km d^{-1} less than during spring migration, on average. Slower speeds in raptor fall migration could be linked to several factors, including warmer weather on the breeding grounds and along migration routes due to climate change resulting in migration delays, or unfavorable wind conditions resulting in slower, longer fall migration (Therrien et al. 2017, Brisson-Curadeau et al. 2020). However, many other species of birds have exhibited shorter, faster fall migrations relative to spring migration and it has been suggested that these differences are due, in part, to species-specific physiological requirements and/or migration-specific weather conditions (e.g., Carneiro et al.

2019, Deng et al. 2019). More research looking at weather patterns and climatic shifts across migration routes and stopover locations for harriers in this study is needed to better understand underlying mechanisms for migration timing.

Migratory harriers followed similar routes for both spring and fall migrations through central to northeast California, Oregon, and Washington, as well as through the intermountain region of British Columbia and Alaska. No birds migrated along the coast except the Alaska breeding birds and only once they reached Alaska. One Alaska bird only migrated along the north coast of the Cook Inlet during spring migration right before approaching her breeding area, while the other Alaska bird migrated along the coast during the first spring migration starting at the Cross Sound of the Alexander Archipelago in southeastern Alaska and returning to an inland route after passing Anchorage. This individual used inland migration routes for her return fall migration, and both spring and fall migrations the following year. This is consistent with spring migration route trends observed by Mindell and Mindell (1984) who observed most harriers migrating through inland routes of the intermountain regions of Alaska, with the second most common route along the southeastern coast of Alaska. Given our results, we believe the previous suggestion that harriers are broad-front migrants relative to other species due to their low detectability at most migration monitoring stations (Goodrich and Smith 2008) is more a reflection of where these stations are located, which may not adequately capture harrier migration. Harriers clearly select wetland habitat during migration in the West and no Western migration monitoring stations are located along migratory routes with significant wetland habitat. Harriers may also migrate at lower altitudes than other raptors (Smith et al. 2020), whereas most migration monitoring sites are located at high-altitude ridges and funnel points. Raptor migration monitoring stations in the West are largely located in the Intermountain and Rocky Mountain flyways, which are comprised almost entirely of Great Basin Desert habitat in the lower 48 United States (Hoffman and Smith 2003, Smith et al. 2008, see maps therein). The only migration stations located in the Pacific Flyway are the Golden Gate Raptor Observatory, which is located directly on the coast in the Marin Headlands of CA, and two Hawkwatch International sites in Bonney Butte, OR, and Chelan Ridge, WA, which are both located at high-altitude west-central locations. Though population trends continue to decline across most Western migration sites (Smith et al. 2008), because harriers are often not highly detected their overall population estimates may be biased low. Raptor migration monitoring stations are invaluable to understanding population trends and migration timing for many species (e.g., Binford 1979, Titus and Fuller 1990, McIntyre and Ambrose 1999, Goodrich and Smith 2008, van Buskirk 2012, Therrien et al. 2017), but species like harriers with unique ecological requirements and life history traits may require more specialized monitoring sites for accurate migration population monitoring.

We found strong selection for wetland habitat across the entire annual cycle (nest sites, stopover sites, and wintering area), which is consistent with known habitat preferences of harriers in other studies (Smith et al. 2020). Wetland habitat is clearly important for nest sites overall due to its suitable vegetation density and structure (Chapter 1), but there is a significant difference between short- and long-distance migrants, with long-distance migrants using far less wetland habitat than short-distance migrants. Only two of six long-distance migrants used wetland habitat as the dominant habitat type at nest sites. The remaining four used either cultivated (two) or shrub habitat (two). This may reflect true selection differences between these populations, or it may simply reflect the lack of suitable wetland habitat at northern latitudes. Cultivated habitat was positively selected at winter sites only, which could indicate a shift in prey populations during winter months. Though we did not formally quantify crop types within used cultivated habitat, visual inspection of landcover maps indicate most cultivated habitat selected was alfalfa, wheat, and hay/pasture. Harriers are known to forage in cultivated crops like alfalfa, as well as pasture or idled grasslands in winter in other populations (Littlefield and Johnson 2005, Pandolfino et al. 2011). These crop types are regularly irrigated with limited ground disturbance, which often support more stable rodent populations and likely explain the selection of these habitat types by harriers in the winter. Grassland and shrub habitat were positively selected during both spring and fall migration suggesting habitat selection may be more general across migration, which is consistent with the need to refuel quickly. Overall, wetland habitat is still the most consistent habitat type selected by harriers, highlighting the importance of this habitat type in harrier annual cycle ecology.

An important finding from our study is that harriers are very clearly non-urban raptors that avoid human development and disturbance across their annual cycle. Stopover locations were scattered across the landscape and appeared individual to each migratory route, though some harriers did use the same stopover sites as other harriers. The shared commonality between these locations, including breeding and wintering areas, is that they are all in either remote wilderness areas, rural agricultural areas, or on protected state wildlife areas and federal national wildlife refuges with wetland habitat. In the Pacific Flyway, much of the remaining wetland habitat is on wildlife areas and refuges. In this study, harriers used nearly all these areas at some point during their annual cycle, highlighting the importance of these areas to harrier population perseverance. Though most of these areas are managed for shorebirds and waterfowl (Stralberg et al. 2011), and harriers seem to benefit from these management practices, a future step would be to determine which management strategies maximize benefits to waterfowl, shorebirds, harriers, and other species alike. Further support for the need for a more holistic ecosystem management approach is that rice agriculture does not appear to benefit harriers in the way that it acts as surrogate wetland habitat for waterfowl, shorebirds, and other wetland-associated species (Elphick and Oring 1998, Bird et al. 2000, Strum et al. 2013). This suggests that protected wildlife areas and refuges may be even more important to harriers than they are for other wetland-dependent species.

5. Management Implications

Harriers targeted remote wilderness, rural agriculture, and protected state and federal lands across Western North America. Ensuring suitable wetland habitat that supports robust rodent populations across these areas is one management action conservationists can promote to support migratory harrier populations. Where this may be challenging in remote wilderness and agricultural areas, managers have direct control over habitat management on state and federal lands. Shifting management plan frameworks from single-species or species groups (waterfowl, shorebirds) to holistic, ecosystem-based management plans that encompass the dynamic needs of a variety of species is needed at the state and federal levels. Fine-scale habitat selection, prey selection, and reproductive ecology research for harriers using each wildlife area and national wildlife refuge across their annual cycle will provide area-specific data needed to focus management actions. This may seem unfeasible, but large-scale waterfowl- and shorebird-specific focused research has been conducted for decades across Flyways in North America through organizations like California Waterfowl, Ducks Unlimited, and The National Audubon Society. And a network of migration monitoring stations already exists via several raptor-specific organizations, like Hawkwatch International. Incorporating the annual waterfowl and shorebird nest-monitoring framework into raptor organizations could be a promising solution to data-gaps needed to make population-wide conservation and management plans for harriers.

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