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RESEARCH ARTICLE

Foraging ecology of a reintroduced population of breeding Bald Eagles on the Channel Islands, California, USA, inferred from prey remains and stable isotope analysis

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ABSTRACT

Successful management of reintroduced populations requires recognizing that ecological conditions may have changed between extirpation and reintroduction. For example, characterizing dietary patterns of generalist apex predators in the past and present can help to define how their functional role may change as translocated populations grow. We identified prey remains collected from Bald Eagle (*Haliaeetus leucocephalus*) nests and used carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope analysis to quantify diet composition of the recently reintroduced Bald Eagle population on the Channel Islands off southern California, USA. We collected >6,000 prey items from recently occupied nests on Santa Catalina, Santa Rosa, Santa Cruz, and Anacapa islands in 2010 and 2011. Prey identification and stable isotope analysis yielded similar results and showed that eagles on Santa Catalina Island consumed a high proportion (~60%) of marine fish and a lower proportion (25–30%) of seabirds, while their counterparts on the Northern Channel Islands consumed equal proportions (~40–45%) of these prey types. Terrestrial resource use was low with the exception of eagles from one nest on Santa Catalina Island, where eagles primarily consumed ground squirrels and freshwater fish. We suggest that a combination of natural and anthropogenic factors is responsible for the interisland differences in Bald Eagle diet. Bald Eagle interactions with a robust recreational fishery off Santa Catalina Island may enhance access to fish species that are not available to eagles on the Northern Channel Islands, where the availability of breeding seabirds is far greater. The proportion of seabirds consumed by eagles on the Northern Channel Islands today is similar to that consumed by eagles from this region historically and prehistorically. This suggests that the restoration of breeding seabirds on the Channel Islands will benefit the long-term viability of eagle populations in the northern archipelago.

Keywords: raptors, seabirds, reintroduction, stable isotope analysis, $\delta^{13}C$, $\delta^{15}N$

Ecología de forrajeo de una población reintroducida de individuos reproductivos de *Haliaeetus leucocephalus* en las Islas del Canal, California, inferida a partir de restos de presas y análisis de isótopos estables

RESUMEN

El manejo exitoso de poblaciones reintroducidas requiere reconocer que las condiciones ecológicas pueden haber cambiado entre el momento de extirpación y de reintroducción. Por ejemplo, la caracterización de los patrones de la dieta pasada y presente de los depredadores generalistas tope ayuda a definir como su rol funcional puede cambiar a medida que crecen las poblaciones relocalizadas. Identificamos restos de presas recolectados en nidos de *Haliaeetus leucocephalus* y empleamos análisis de isótopos estables de carbono ($\delta^{13}C$) y nitrógeno ($\delta^{15}N$) para cuantificar la composición de la dieta de una población recientemente reintroducida de *H. leucocephalus* en las Islas del Canal en el sur de California. Recolectamos >6,000 ítems de presas en nidos recientemente ocupados en las Islas Santa Catalina, Santa Rosa, Santa Cruz y Anacapa en 2010 y 2011. La identificación de las presas y los análisis de isótopos estables brindaron resultados similares y mostraron que las águilas en Catalina consumieron una alta proporción (~60%) de peces marinos y 25–30% de aves marinas, mientras que sus homólogos en las islas del norte consumieron proporciones iguales (~40–45%) de estos tipos de presas. El uso de recursos terrestres fue bajo con excepción de un nido en Catalina, en el que las águilas consumieron principalmente ardillas terrestres y peces de agua dulce. Sugerimos que una combinación de factores naturales y antropogénicos es responsable de las diferencias entre islas en la dieta de *H. leucocephalus*. Las interacciones de *H. leucocephalus* con una actividad de pesca recreativa muy activa en los alrededores de Catalina puede permitir acceder a especies de peces que no están disponibles para las águilas en las islas del norte, donde la disponibilidad de aves marinas reproductivas es mucho mayor. La proporción de aves marinas

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consumidas actualmente por las águilas en las islas del norte es similar al consumo histórico y prehistórico de las águilas en esta región. Esto sugiere que la restauración de aves marinas reproductivas en las Islas del Canal beneficiará la viabilidad a largo plazo de las poblaciones de águilas en el archipiélago del norte.

Palabras clave: análisis de isótopos estables, aves marinas, rapaces, reintroducción, $\delta^{13}C$, $\delta^{15}N$

INTRODUCTION

Our understanding of the distribution and ecology of animals is confounded by centuries, if not millennia, of human harvest, compounded by more recent pollution, habitat alteration, and climate change (Pauly et al. 1998, Jackson et al. 2001, Estes et al. 2011). Despite conservation efforts, many large-bodied apex predators currently occupy a fraction of their past ranges. Translocation is sometimes used to reestablish these species in previously occupied areas (e.g., Sharpe 2007, Esslinger and Bodkin 2009, Baker et al. 2011, Deguchi et al. 2014). Even when historical, archaeological, and paleontological information is available to characterize a species' former presence, abundance, and/or ecological role, essential ecological conditions such as habitat quality and food supply may have changed since a predator's local extinction in the area slated for translocation. Moreover, human alteration of the environment may have generated novel sources of prey that were not exploited by past populations. Further, in cases where conventional prey contains contaminants or is also of conservation concern, continued monitoring of both predator and potential prey is a necessary component of successful management. Comparison of past ecological information with new data from a translocated population can provide valuable insights for understanding the success and ecological impact of a reintroduced population.

Bald Eagles (*Haliaeetus leucocephalus*) were once a familiar apex predator and scavenger on all 8 of the Channel Islands off southern California, USA. As a result of both direct (e.g., hunting, egg collection) and indirect (e.g., pesticide application) negative interactions with humans, Bald Eagles disappeared from the Channel Islands by the mid-1960s (Kiff 1980). The harmful effects of contaminant exposure played an especially important role in the local demise of eagles and their prey in the archipelago, because millions of kilograms of dichlorodiphenyl trichloroethane (DDT) and polychlorinated biphenyls (PCBs) were discharged into the ocean directly adjacent to Santa Catalina Island (Eagenhouse et al. 2000). Despite the legacy of high contaminant loads in the marine food webs on which resident Bald Eagles primarily depend, over the past 35 years a reintroduction program has established breeding eagles on 5 of the 8 Channel Islands where they historically bred: Santa Catalina, San Clemente, Santa Cruz, Santa Rosa, and Anacapa islands. As this population continues to grow and expand to other islands in the archipelago, a thorough understanding of Bald Eagle dietary habits may benefit management of both eagles and their prey by identifying: (1) the most important prey utilized by the recovering eagle population and whether this differs from the diet of historic (1800–1970 A.D.) and prehistoric (before 1800 A.D.) eagle populations that occurred at higher densities than their modern counterparts; (2) whether commonly consumed prey are vectors of contaminant exposure to eagles (Garcelon et al. 1994a, 1994b, Sharpe and Garcelon 1999, Blasius and Goodmanlowe 2008, Pagel et al. 2012); and (3) any potential impacts that a growing eagle population may have on other recovering wildlife populations (e.g., seabirds or island foxes [*Urocyon littoralis*]) in the archipelago.

Bald Eagles are opportunistic generalists that consume a wide variety of prey via direct capture, scavenging, and/or kleptoparasitism (Stalmaster 1987, Buehler 2000). When freshwater or marine fish are locally available, eagles generally favor them over other classes of prey (Stalmaster 1987). In the Channel Islands, direct observation and identification of prey remains from the nests of reintroduced eagles show that, in addition to marine fish, seabirds are also frequently consumed. On Santa Catalina Island (hereafter, Catalina) from 1991 to 1998, of total prey deliveries to nests, on average 86% were marine fish, 10% were seabirds, and 4% were terrestrial mammals (Sharpe and Garcelon 1999). There are no dietary studies available for the reintroduced eagles breeding on the Northern Channel Islands (hereafter, NCI, and referring to Santa Cruz, Santa Rosa, and Anacapa islands), but previous research on a historic Bald Eagle nest on San Miguel Island in the NCI showed that eagles breeding there in the first half of the 20th century consumed a higher proportion of seabirds than their modern counterparts on Catalina (Collins et al. 2005, Erlandson et al. 2007, Newsome et al. 2010). Today, and presumably in the past, the NCI host a greater diversity and abundance of breeding seabirds than Catalina (Hunt et al. 1980, Sowls et al. 1980, Carter et al. 1992), so it is anticipated that seabirds will be an important source of prey for the reintroduced eagle population on the NCI.

Establishing whether the reintroduced Bald Eagles on the NCI are consuming seabirds, as their historic counterparts did, and which seabird species are targeted, is important for both eagle and seabird conservation in the Channel Islands. Seabirds, whose local populations declined in the mid-20th century for some of the same reasons as Bald Eagle populations (e.g., pesticides), are also the focus of intensive conservation programs on the

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Channel Islands. Today, more than a dozen species of seabird breed on the archipelago. Another abundant but potentially problematic source of food for eagles in the archipelago is marine mammal carrion, especially that of California sea lions (*Zalophus californianus*) and northern elephant seals (*Mirounga angustirostris*), whose local breeding colonies each total >100,000 individuals (Carretta et al. 2013). Like seabirds, marine mammals forage at a higher trophic level than marine fish and thus have relatively higher contaminant loads (Blasius and Goodmanlowe 2008); consistent consumption of marine mammals or seabirds may negatively affect eagle breeding success (Sharpe and Garcelon 1999).

Because eagles are highly mobile and have large home ranges, quantification of eagle diets is difficult. Traditional analyses have relied on a variety of techniques, such as: (1) direct observation of prey items returned to the nest and adjacent perches during the breeding season; (2) examination of prey in regurgitated pellets collected at communal roosts; (3) direct observation of foraging; and (4) identification of prey remains found in nests after the breeding season (Mersmann et al. 1992, Sharpe and Garcelon 1999, Buehler 2000). Perhaps the most comprehensive approach is to couple traditional methods with stable isotope analysis of eagles and their putative prey, which provides a time-integrated estimate of ingested biomass (Weiser and Powell 2011, Resano-Mayor et al. 2014).

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope analysis of animal tissues has become an established method for characterizing animal resource and habitat use (Kelly 2000, Koch 2007, Newsome et al. 2007a), and is especially useful for distinguishing between marine and terrestrial resource use by consumers because of baseline differences in the isotopic composition of primary producers in marine vs. terrestrial ecosystems. Sulfur isotope ($\delta^{34}S$) analysis has also been used to examine marine vs. terrestrial resource use by consumers in coastal settings (Peterson and Fry 1987, Hesslein et al. 1991); however, the application of this isotope system is limited because it is analytically more intensive and expensive in comparison with $\delta^{13}C$ and $\delta^{15}N$ analysis. In California, primary productivity in coastal terrestrial ecosystems is dominated by plants that use the C_3 photosynthetic pathway (Suits et al. 2005), resulting in food webs characterized by relatively low $\delta^{13}C$ values ranging from −22‰ to −28‰ (Craig 1953). Coastal marine ecosystems, in contrast, are dominated by a combination of micro- and macroalgae that have higher $\delta^{13}C$ values of −16‰ to −20‰ (Page et al. 2008). For nitrogen, field- and laboratory-based studies have established that there is a systematic increase in $\delta^{15}N$ values of ~3–5‰ per trophic level in both marine and terrestrial ecosystems (Vanderklift and Ponsard 2003). Because coastal marine ecosystems contain a greater number of trophic levels than terrestrial ecosystems, marine apex predators have higher $\delta^{15}N$ values than their terrestrial counterparts (Kelly 2000).

In this study, we coupled the identification of prey collected from recently occupied Bald Eagle nests with $\delta^{13}C$ and $\delta^{15}N$ analysis to quantify the diet of reintroduced Bald Eagles that breed in different regions of the Channel Island archipelago, across which prey availability varies due to a combination of natural and anthropogenic factors. We used faunal identification to quantify the diversity of prey utilized by eagles and stable isotope analysis to quantify the relative biomass proportions of general prey types (e.g., marine fish vs. seabirds) consumed by adults and nestlings on different islands in the archipelago. In addition, we compared modern dietary patterns with those from historic and prehistoric Bald Eagle populations on the Northern Channel Islands (Collins et al. 2005, Erlandson et al. 2007, Newsome et al. 2010) to assess how the prey base of this generalist predator has been influenced by human activities in the archipelago, including shifts in land use practices, intensification of commercial and recreational fishing, and conservation programs that protect marine wildlife consumed by eagles.

METHODS

Study Area and Field Collections

Nests used by the reintroduced Bald Eagle population on Catalina (33.383°N, 118.417°W, $n = 9$ in 2010 and $n = 5$ in 2011), Santa Cruz (34.004°N, 119.726°W, $n = 4$ in 2011), Santa Rosa (33.966°N, 120.108°W, $n = 2$ in 2010), and Anacapa (34.011°N, 119.425°W, $n = 1$ in 2011) islands were examined in Oct–Nov of 2010 and 2011 for prey remains and eagle feathers. We visited nests on Santa Cruz only in 2011 because of permit issues, on Santa Rosa only in 2010 because both nests on the island failed in 2011, and on Anacapa only in 2011 because that was the first year in which Bald Eagles nested on that island. When necessary, we used a professional climber to access eagle nests on rock pinnacles, ledges, cliff faces, and in trees. All prey remains (bones, teeth, otoliths, fish spines and scales, and feathers) and eagle remains (feathers) visible on and within the outer stick structure of the nest, within the nest cup, and in the immediate vicinity of the nest site were collected by hand and stored in plastic bags for transport to the laboratory for identification and sampling. The lining of the nest cup was carefully examined, and any accumulated sediment in the bottom of the nest cup was sifted with a 1.5 mm (1/16 inch) mesh screen to recover smaller prey remains. The nest lining was returned to its original condition following the recovery of prey remains from the inside of the nest cup. The stick structure of each nest was not disassembled in the process of recovering prey and eagle remains.

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Nestling feathers were collected during annual banding efforts on Catalina, Santa Rosa, and Santa Cruz islands in May–June of 2010 and 2011. During capture, the sex of each eaglet was determined by morphological measurements (Bortolotti 1984, Garcelon et al. 1985), and 3 contour feathers were collected and stored in a paper envelope until analysis. Adult feathers were opportunistically collected from nests and perches on Catalina, Santa Rosa, and Santa Cruz islands in Oct–Nov of 2010 and 2011.

Prey Identification

In the laboratory, prey remains were identified to the lowest identifiable taxonomic level—class, order, family, genus, or species—by comparing diagnostic elements such as bones, teeth, and otoliths with identified specimens in the research collections at the Santa Barbara Museum of Natural History (Santa Barbara, California; see Collins et al. [2005] for a list of the bone elements used for identification of birds, fish, mammals, and reptiles). Fragmentary, nondiagnostic specimens were identified as undifferentiated mammal, reptile, bird, or fish.

Faunal remains that were thought to be incidental rather than preyed upon by eagles were eliminated from all further analyses of eagle diet. Taxa considered to be incidental remains included: (1) taxa that likely were in the crop, stomach, or gut of seabirds brought to the nest to feed nestlings (most of the smaller invertebrate remains); (2) small birds (passerines) and lizards that were potentially captured by other birds such as Peregrine Falcons (*Falco peregrinus*), American Kestrels (*Falco sparverius*), Red-tailed Hawks (*Buteo jamaicensis*), and Common Ravens (*Corvus corax*) that frequently perch on eagle nests during the late summer and fall when eagles are not defending nest sites; and (3) small invertebrates (land snails, beetles, and insect pupae) that either crawled into the nest structure or were attached to marine algae lining the nest cup. It was difficult to know whether the remains of small mammals (mice and rats) and some of the small fish found in a nest were also incidental remains or were the result of actual eagle predation; we included these as eagle prey.

Following the removal of incidental material, we quantified the faunal remains as: (1) the number of individual specimens (NISP), calculated by counting the total number of elements identified to each taxon; and (2) minimum number of individuals (MNI), determined by the greatest number of unique elements identified per taxon. To calculate MNI, we used the total number of sided, nonrepetitive postcranial and cranial elements from a particular taxon, or in some cases the number of fish vertebrae identified divided by an average number of vertebrae for that taxon (Rick et al. 2001). Prey remains were initially quantified to MNI for each nest site or identified taxonomic category, and were then lumped and quantified to MNI by island or region.

Stable Isotope Analysis

We removed all vane material from the rachis of each nestling body feather and then homogenized each feather by cutting the sample into small pieces with surgical scissors. For adult primary and secondary feathers, we removed 3 subsamples for isotopic analysis, 1 each near the tip, the base, and the middle of each feather, and calculated the mean $\delta^{13}C$ and $\delta^{15}N$ value of these 3 subsamples to estimate isotope values for each adult eagle. Feather subsamples were treated with a 2:1 chloroform:-methanol solution to remove surface contaminants. To isolate bone collagen from prey remains, a small bone fragment was demineralized in 0.5N HCl for ~36 hr at ~5°C. Bone collagen samples were then treated with 3 sequential ~24 hr soaks in a 2:1 chloroform:methanol mixture to remove lipids, rinsed in deionized water, and lyophilized.

An ~0.5 mg subsample of dried keratin (from feathers) or bone collagen was sealed in a tin capsule and analyzed using a Carlo Erba NC2500 or Costech 4010 elemental analyzer (Bremen, Germany) interfaced with a Thermo Finnigan Delta Plus XL mass spectrometer (Bremen, Germany) at the University of Wyoming Stable Isotope Facility (Laramie, Wyoming, USA). Stable isotope results are expressed as δ values, calculated as $\delta^{13}C$ or $\delta^{15}N = 1000 * [(R_{sample} / R_{standard}) - 1]$, where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and standard, respectively. The standards are Vienna Pee Dee Belemnite (VPDB) limestone for carbon and atmospheric N_2 for nitrogen. δ values are expressed as parts per thousand or per mill (‰). As a control for the quality of feather keratin and bone collagen, we measured the carbon-to-nitrogen concentration, reported as a [C]/[N] ratio, of each sample and compared it to the theoretical atomic [C]/[N] ratio of each tissue.

Statistical Tests and Stable Isotope Mixing Models

We used a one-way analysis of variance (ANOVA) and a post-hoc Tukey honest significant difference (HSD) test to assess differences in $\delta^{13}C$ and $\delta^{15}N$ values among major prey types such as marine fish, seabirds, and terrestrial resources, and between sexes of eagle nestlings. We then used the Stable Isotope Analysis in R (SIAR) mixing model (Parnell et al. 2010) to quantify the proportion of marine fish, seabirds, and terrestrial resources in nestling and adult eagle diets. The Bayesian SIAR model allows for the assessment of greater than $n + 1$ sources when using n isotope systems; however, the inclusion of a large number of potential prey sources often yields cumbersome results (Phillips 2012). Our goal was to quantify the consumption of general prey types by eagles in each region, so we

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tailored our models specifically to the availability and isotopic composition of local prey sources available to eagles on Catalina or the NCI.

Because we compared different tissues between eagles (feathers) and potential prey (bone collagen), we had to account for both tissue-specific and trophic discrimination when estimating a discrimination factor to use in the SIAR mixing models. A controlled feeding experiment on captive Bald Eagles at the San Francisco Zoo examined trophic discrimination ($\Delta^{13}C_{tissue\text{-}diet}$ or $\Delta^{15}N_{tissue\text{-}diet}$) of feathers for both adults and nestlings (J. Rempel personal communication). Nestlings had lower $\delta^{15}N$ trophic discrimination factors, a pattern also found in other animals (Vanderklift and Ponsard 2003), which is caused by a decrease in nitrogen isotope discrimination during periods of rapid growth. Based on this pattern, we used a $\Delta^{15}N_{tissue\text{-}diet}$ discrimination factor of 3.0 ± 0.5‰ for adults and 2.0 ± 0.5‰ for nestlings regardless of tissue type; $\Delta^{15}N_{tissue\text{-}diet}$ discrimination factors do not vary significantly among tissues. For $\delta^{13}C$, bone collagen has a higher $\Delta^{13}C_{tissue\text{-}diet}$ discrimination factor than feathers (Koch 2007, Caut et al. 2009); thus, we used a slightly negative discrimination factor (−1.0 ± 0.5‰) between prey and consumer (feather) bone collagen in our SIAR mixing models to account for both tissue-specific and trophic discrimination.

RESULTS

Conventional Diet Analysis

A total of 6,265 prey remains from 72 species and 38 families was recovered from recently occupied Bald Eagle nests on the Channel Islands (Table 1). Of the 546 individuals identified, 279 (51%) were fish, 229 (42%) were birds, and 38 (7%) were mammals (Table 1). The relative proportions of general prey types as well as the diversity and abundance of species recovered varied between NCI and Catalina nests (Figure 1). NCI nests contained 43% (81 MNI) fish, 54% (101 MNI) birds, and 3% (6 MNI) mammals, while nests on Catalina contained 55% (198 MNI) fish, 36% (128 MNI) birds, and 9% (32 MNI) mammals (Table 1, Figure 1).

The most important families of fish recovered from NCI and Catalina nests were rockfish (Scorpaenidae), toadfish (Batrachoididae), and surfperch (Embiotocidae; Table 1). A greater diversity (16 families and at least 22 species) and abundance (198 MNI) of fish were recovered from nests on Catalina in comparison with NCI nests (7 families, 11 species, 81 MNI; Table 1). The most important bird families found in Channel Islands eagle nests were gulls (Laridae, 14% MNI), cormorants (Phalacrocoracidae, 8%), alcids (Alcidae, 7%), fulmars and shearwaters (Procellariidae, 6%), and waterfowl (Anatidae, 2%). The relative proportions of these 5 bird families varied slightly in nests from Catalina vs. the NCI (Table 1, Figure 1). Cormorants and alcids were more abundant in NCI nests, while gulls, shearwaters, waterfowl, ravens, and grebes were more abundant in Catalina nests (Table 1, Figure 1). Ungulates were the most abundant mammal in eagle nests on both the NCI (2%) and Catalina (3%). Rodents (California ground squirrels [*Spermophilus beecheyi*] and black rats [*Rattus rattus*]) were only found in Catalina nests, while western spotted skunks (*Spilogale gracilis*) were only found in NCI nests (Table 1). Island foxes comprised 0.3% and 0.5% of prey recovered from Catalina and NCI nests, respectively.

Stable Isotope Analysis

The use of stable isotope analysis to quantify resource proportions via mixing models requires potential prey types to have distinct $\delta^{13}C$ and/or $\delta^{15}N$ values. Isotopic patterns among potential eagle prey generally conformed to expectations, and we found differences in mean $\delta^{13}C$ and/or $\delta^{15}N$ values between marine and terrestrial prey, as well as among marine fish and seabirds (Table 2, Figure 2). Given the high diversity of potential prey, we grouped prey by family or genus and subdivided them into the 2 regions (Catalina and NCI). As expected, marine resources (fish and seabirds) had higher $\delta^{13}C$ and $\delta^{15}N$ values than terrestrial resources (ungulates, rodents, and freshwater fish) for both Catalina ($\delta^{13}C$: $F_{1,293} = 630.5$, $P < 0.001$; $\delta^{15}N$: $F_{1,293} = 796.0$, $P < 0.001$) and the NCI ($\delta^{13}C$: $F_{1,175} = 721.0$, $P < 0.001$; $\delta^{15}N$: $F_{1,175} = 795.7$, $P < 0.001$). In addition, seabirds had higher $\delta^{13}C$ and $\delta^{15}N$ values than marine fish for both Catalina ($\delta^{13}C$: $F_{1,257} = 7.2$, $P = 0.008$; $\delta^{15}N$: $F_{1,257} = 41.4$, $P < 0.001$) and the NCI ($\delta^{13}C$: $F_{1,141} = 88.9$, $P < 0.001$; $\delta^{15}N$: $F_{1,141} = 119.6$, $P < 0.001$).

At the family and genus level, we found significant isotopic differences among potential eagle prey; however, the isotope system ($\delta^{13}C$ or $\delta^{15}N$) that showed significant differences was not consistent between regions. On Catalina, $\delta^{15}N$ values were the most useful isotope system to discriminate among prey families or genera. The following comparisons among Catalina prey are based on a one-way ($\delta^{15}N$) ANOVA ($F_{1,257} = 25.1$, $P < 0.05$). On Catalina, gulls had significantly higher $\delta^{15}N$ values than all types of marine fish. All other seabird families did not have significantly different $\delta^{15}N$ values from rockfish, midshipman, or kelp bass. Surfperch, sheepheads, flyingfish, and miscellaneous small fish had significantly lower $\delta^{15}N$ values than seabirds and other marine fish with the exception of kelp bass.

On the NCI, patterns among families or genera of Bald Eagle prey were detectable with both $\delta^{13}C$ and $\delta^{15}N$ values. For $\delta^{13}C$ ($F_{1,141} = 24.3$, $P < 0.05$), rockfish and surfperch had higher values than any other families or genera of marine fish or seabirds. All other families and genera of seabirds or marine fish had similar $\delta^{13}C$ values. For $\delta^{15}N$ ($F_{1,141} = 29.1$, $P < 0.05$), alcids had higher $\delta^{15}N$ values than any other marine fish or seabird families or genera. Gulls

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TABLE 1. Animal remains found in Bald Eagle nests on the Channel Islands, California, USA, grouped by region: Santa Catalina Island and the Northern Channel Islands (Santa Rosa, Santa Cruz, and Anacapa islands). Data are presented as the minimum number of individuals (MNI), with the number of identifiable specimens (NISP) in parentheses. Families are listed in order of importance.

	Santa Catalina Island		Northern Channel Islands		All islands	
Common name (Family)	MNI (NISP)	%MNI	MNI (NISP)	%MNI	MNI (NISP)	%MNI
Fish						
Rockfish (Scorpaenidae)	78 (827)	21.8	14 (414)	7.4	92 (1,241)	16.8
Toadfish (Batrachoididae)	14 (75)	3.9	41 (184)	21.8	55 (259)	10.1
Flyingfish (Exocoetidae)	45 (252)	12.6			45 (252)	8.2
Surfperch (Embiotocidae)	12 (49)	3.4	21 (458)	11.2	33 (507)	6.0
Sea bass (Serranidae)	17 (161)	4.7			17 (161)	3.1
Sunfish, Bass (Centrarchidae)	3 (53)	0.8			3 (53)	0.5
Wrasses (Labridae)	6 (11)	1.7	1 (1)	0.5	7 (12)	1.3
Croakers (Sciaenidae)	6 (20)	1.7			6 (20)	1.1
Sea chub (Kyphosidae)	5 (16)	1.4			5 (16)	0.9
Tuna, Mackerel (Scombridae)	4 (42)	1.1			4 (42)	0.7
Flounders (Bothidae)	3 (39)	0.8	1 (75)	0.5	4 (114)	0.7
Cat sharks (Scyliorhinidae)			2 (2)	1.1	2 (2)	0.4
Thornbacks (Platyrhinidae)	1 (1)	0.3			1 (1)	0.2
Smoothhounds (Triakidae)	1 (65)	0.3			1 (65)	0.2
Stingrays (Dasyatidae)	1 (1)	0.3			1 (1)	0.2
Moray eels (Muraenidae)	1 (2)	0.3			1 (2)	0.2
Silversides (Atherinidae)			1 (25)	0.5	1 (25)	0.2
Damselfish (Pomacentridae)	1 (2)	0.3			1 (2)	0.2
Unidentified fish	(877)		(159)		(1,036)	
Fish, total	198 (2,493)	55.3	81 (1,318)	43.1	279 (3,811)	51.1
Birds						
Gulls (Laridae)	45 (257)	12.6	31 (326)	16.5	76 (583)	13.9
Cormorants (Phalacrocoracidae)	17 (158)	4.7	26 (333)	13.8	43 (491)	7.9
Auks, Murres, Puffins (Alcidae)	18 (179)	5.0	21 (268)	11.2	39 (447)	7.1
Fulmars, Shearwaters (Procellariidae)	26 (195)	7.3	8 (176)	4.3	34 (371)	6.2
Ducks, Geese (Anatidae)	7 (48)	2.0	4 (11)	2.1	11 (59)	2.0
Crows, Jays (Corvidae)	5 (28)	1.4	1 (21)	0.5	6 (49)	1.1
Grebes (Podicipedidae)	5 (34)	1.4	2 (2)	1.1	7 (36)	1.3
Loons (Gaviidae)	3 (4)	0.8	3 (15)	1.6	6 (19)	1.1
Pelicans (Pelecanidae)			3 (49)	1.6	3 (49)	0.5
Shorebirds (Charadriidae)	1 (1)	0.3	1 (42)	0.5	2 (43)	0.4
Storm-Petrels (Hydrobatidae)	1 (1)	0.3			1 (1)	0.2
Tropicbirds (Phaethontidae)			1 (2)	0.5	1 (2)	0.2
Unidentified birds	(142)		(99)		(241)	
Birds, total	128 (1,047)	35.8	101 (1,344)	53.7	229 (2,391)	41.9
Mammals						
Deer, Elk (Cervidae)	12 (16)	3.4	3 (5)	1.6	15 (11)	2.7
Ground squirrels (Sciuridae)	8 (9)	2.2			8 (9)	1.5
Eared seals (Otariidae)	6 (16)	1.7	1 (2)	0.5	7 (18)	1.3
Rats, Mice (Muridae)	3 (5)	0.8			3 (5)	0.5
Island foxes (Canidae)	1 (6)	0.3	1 (4)	0.5	2 (10)	0.4
True seals (Phocidae)	1 (3)	0.3			1 (3)	0.2
Spotted skunks (Mephitidae)			1 (1)	0.5	1 (1)	0.2
Cattle, Sheep, Goats (Bovidae)	1 (1)	0.3			1 (1)	0.2
Unidentified mammals	(5)				(5)	
Mammals, total	32 (61)	8.9	6 (12)	3.2	38 (63)	7.0
Grand total	358 (3,601)	100.0	188 (2,674)	100.0	546 (6,265)	100.0

and cormorants had significantly higher $\delta^{15}N$ values than rockfish and surfperch. Fulmars and shearwaters had similar $\delta^{15}N$ values to all other groups except for alcids and surfperch. Lastly, midshipman had similar $\delta^{15}N$ values to all other groups, except for alcids.

For Bald Eagle nestlings (Table 3), we found no sex-related differences in feather $\delta^{13}C$ ($F_{1,27} = 0.5$, $P > 0.10$) or $\delta^{15}N$ ($F_{1,27} = 0.3$, $P > 0.10$). Likewise, we found no year effects in $\delta^{13}C$ ($F_{1,27} = 0.006$, $P > 0.10$) or $\delta^{15}N$ (feather: $F_{1,27} = 1.9$, $P > 0.10$) of either tissue. Nestlings from

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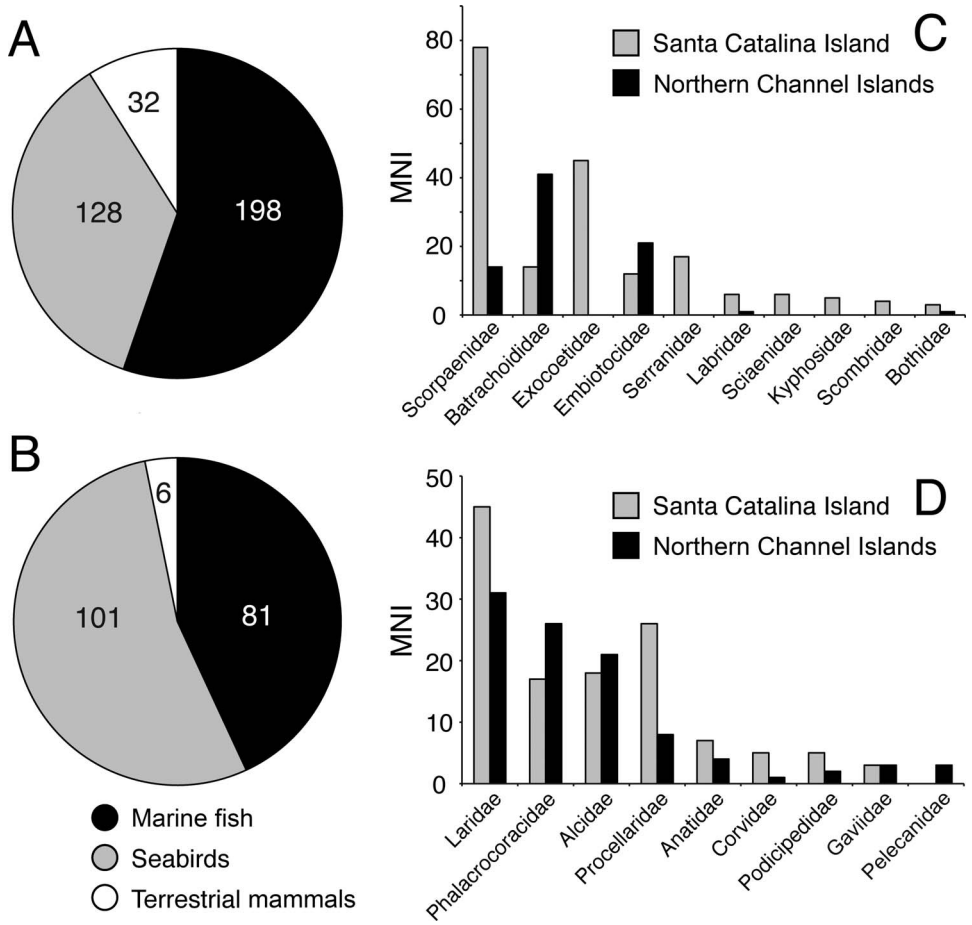


FIGURE 1. Relative proportions of major prey types identified from Bald Eagle nests on (**A**) Santa Catalina Island and (**B**) the Northern Channel Islands, California, USA, based on the minimum number of individuals (MNI). MNI frequency distributions present the diversity of (**C**) marine fish and (**D**) seabirds identified at the family level found in Bald Eagle nests on Santa Catalina Island (gray bars) and the Northern Channel Islands (black bars). Freshwater fish (Centrarchidae) from Santa Catalina Island (MNI = 3) are not shown.

Catalina had lower mean feather ($F_{1,27} = 18.2$, $P < 0.001$) $\delta^{13}C$ values than their counterparts from the NCI. There were no significant differences in feather $\delta^{15}N$ values ($F_{1,27} = 2.3$, $P > 0.10$) between nestlings from these 2 regions. Due to low sample sizes, we did not test for differences among nestlings from different nests. For Bald Eagle adults (Table 3), after excluding the 2 Catalina eagles that obviously consumed a high proportion of terrestrial resources, eagles from Catalina had significantly lower $\delta^{13}C$ ($F_{1,14} = 10.3$, $P = 0.005$) and slightly lower $\delta^{15}N$ ($F_{1,14} = 3.4$, $P = 0.09$) values than their counterparts from the NCI.

Stable Isotope Mixing Models

For Catalina, we used a mixing model with 4 potential prey sources: seabirds, marine fish (excluding flyingfish), flyingfish, and terrestrial resources (ungulates and rodents); flyingfish were separated from other marine fish because they had significantly different $\delta^{13}C$ and $\delta^{15}N$ values (see Appendix Figure 3 for a $\delta^{13}C$ vs. $\delta^{15}N$ biplot of major prey types used in mixing models for eagles from Catalina and the NCI). Seabirds ($n = 108$) had mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values of –15.6 ± 1.3‰ and 16.3 ± 1.5‰, respectively; marine fish (excluding flyingfish; $n = 117$) had mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values of –14.6 ± 1.0‰ and 15.6 ± 1.1‰, respectively; flyingfish ($n = 32$) had mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values of –17.0 ± 0.7‰ and 13.2 ± 1.1‰, respectively; and terrestrial resources (rodents and deer, $n = 25$) had mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values of –21.0 ± 1.7‰ and 6.0 ± 2.0‰, respectively. For the eagles from the Middle Ranch nest on Catalina near Thompson Reservoir, we added to the model a fifth prey source, freshwater fish ($n = 11$), that had mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values of –24.6 ± 1.8‰ and 9.5 ± 0.8‰, respectively. For the NCI, we used a mixing model with 3 potential prey sources: seabirds, marine fish, and ungulates (deer and elk). Seabirds ($n = 94$) had mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values of –14.8 ± 1.1‰ and 16.4 ± 1.3‰,

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TABLE 2. Mean (SD) bone collagen $\delta^{13}C$ and $\delta^{15}N$ values of major prey types (minimum number of individuals >10) identified from Bald Eagle nests and perches on the Channel Islands, California, USA. Prey types were grouped by region: Santa Catalina Island and the Northern Channel Islands (Santa Cruz, Santa Rosa, and Anacapa).

		Santa Catalina Island			Northern Channel Islands			All islands		
Prey type	Common name, scientific name (*n*)	*n*	$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$
Rockfish	Unidentified, *Sebastes* spp.	66	−14.4 (0.9)	16.1 (0.6)	13	−12.3 (0.7)	14.6 (0.7)	79	−14.1 (1.2)	15.9 (0.8)
Flyingfish	California flying fish, *Cheilopogon pinnatibarbatus californicus*	32	−17.0 (0.7)	13.2 (1.1)	—	—	—	—	—	—
Surfperch	Unidentified, Embioticidae (25) Pile surfperch, *Rhacochilus vacca* (9) Black surfperch, *Embiotoca jacksoni* (7)	12	−14.6 (1.1)	14.3 (0.9)	29	−12.4 (1.3)	13.7 (0.5)	41	−13.1 (1.6)	13.9 (0.7)
Sea bass	Kelp bass, *Paralabrax clathratus* (13) Barred sand bass, *Paralabrax nebulifer* (1)	14	−14.3 (1.2)	15.5 (0.8)	—	—	—	—	—	—
Sunfish	Smallmouth bass, *Micropterus dolomieu* (8) Bluegill, *Lepomis macrochirus* (3)	11	−24.6 (1.8)	9.5 (0.8)	—	—	—	—	—	—
Wrasses (large)	California sheephead, *Semicossyphus pulcher*	6	−14.6 (0.8)	14.2 (1.2)	—	—	—	—	—	—
Midshipman	Unidentified, *Porichthys* spp. (5) Specklefin midshipman, *Porichthys myriaster* (4) Plainfin midshipman, *Porichthys notatus* (4)	8	−15.8 (1.2)	16.1 (1.2)	5	−15.3 (0.6)	15.2 (0.7)	13	−15.6 (1.0)	15.7 (1.1)
Miscellaneous small fish	Sea chub, Kyphosidae (5) Mackerel & Tuna, Scrombridae (4) Wrasses (small), Labridae (2)	11	−15.2 (1.5)	14.3 (1.3)	—	—	—	—	—	—
Gulls	Black-legged Kittiwake, *Rissa tridactyla* (1) Heermann's Gull, *Larus heermanni* (3) Mew Gull, *Larus canus* (2) Western Gull, *Larus occidentalis* (46) California Gull, *Larus californicus* (14) Herring Gull, *Larus argentatus* (5) Glaucous-winged Gull, *Larus glaucescens* (2)	39	−15.2 (1.0)	16.7 (1.6)	34	−14.9 (1.2)	16.3 (1.2)	73	−15.0 (1.1)	16.5 (1.4)
Cormorants	Brandt's Cormorant, *Phalacrocorax penicillatus* (33) Double-crested Cormorant, *Phalacrocorax auritus* (1) Pelagic Cormorant, *Phalacrocorax pelagicus* (18)	18	−14.5 (1.1)	16.4 (1.0)	34	−14.6 (1.1)	16.2 (1.2)	52	−14.6 (1.1)	16.3 (1.1)
Auks, Murres, Puffins	Common Murre, *Uria aalge* (13) Pigeon Guillemot, *Cepphus columba* (3) Cassin's Auklet, *Ptychoramphus aleuticus* (9) Rhinoceros Auklet, *Cerorhinca monocerata* (11) Tufted Puffin, *Fratercula cirrhata* (1)	18	−15.9 (0.9)	16.6 (1.0)	19	−14.7 (0.7)	17.3 (0.8)	37	−15.3 (1.0)	17.0 (0.9)

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TABLE 2. Continued.

Prey type	Common name, scientific name (*n*)	Santa Catalina Island			Northern Channel Islands			All islands		
		n	$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$
Fulmars, Shearwaters	Northern Fulmar, *Fulmarus glacialis* (9)	33	−16.4 (1.3)	15.6 (1.6)	7	−15.6 (1.5)	15.5 (2.2)	40	−16.3 (1.4)	15.6 (1.7)
	Pink-footed Shearwater, *Puffinus creatopus* (11)									
	Sooty Shearwater, *Puffinus griseus* (17)									
	Short-tailed Shearwater, *Puffinus tenuirostris* (2)									
	Black-vented Shearwater, *Puffinus opisthomelas* (1)									
Ungulates	Mule deer, *Odocoileus hemionus* (30)	12	−21.4 (1.8)	5.7 (1.7)	34	−21.7 (1.0)	7.2 (1.5)	46	−21.6 (1.3)	6.8 (1.7)
	Elk, *Cervus canadensis* (16)									
Rodents	California ground squirrel, *Spermophilus beecheyi* (9)	13	−20.7 (1.6)	6.2 (2.3)	—	—	—	—	—	—
	Black rat, *Rattus rattus* (4)									

respectively. Marine fish ($n = 47$) had mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values of −12.7 ± 1.4‰ and 14.1 ± 0.8‰, respectively. Ungulates ($n = 34$) had mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values of −21.7 ± 1.0‰ and 7.2 ± 1.5‰, respectively.

Figure 4 presents a summary of mixing model results for all of the Bald Eagle adults and nestlings that we analyzed, with the exception of eagles from the Middle Ranch nest on Catalina (see below). Appendix Figure 5 shows posterior frequency histograms of source proportions of the major prey types used in the SIAR mixing models for Bald Eagle nestlings and adults from Catalina and the NCI. For Catalina, we combined post hoc the source proportions for marine fish and flyingfish to report a total marine fish proportion. In order of importance, mean source proportions for the nestlings ($n = 16$) from Catalina were 57 ± 4% marine fish (flyingfish: 25 ± 2%; other marine fish: 32 ± 5%), 28 ± 4% seabirds, and 15 ± 7% terrestrial resources (ungulates and rodents). Mean source proportions for the adults ($n = 9$) from Catalina were 61 ± 3% marine fish (flyingfish: 20 ± 3%; other marine fish: 41 ± 4%), 31 ± 2% seabirds, and 8 ± 2% terrestrial resources. Mean source proportions for the nestlings ($n = 10$) from the NCI were 48 ± 4% seabirds, 44 ± 3% marine fish, and 8 ± 2% ungulates. Mean source proportions for the adults ($n = 6$) from the NCI were 47 ± 6% marine fish, 41 ± 8% seabirds, and 12 ± 9% ungulates.

In the calculated mean proportions shown in Figure 3, we did not include results for the Bald Eagles from the Middle Ranch nest on Catalina that consumed a high proportion of terrestrial resources. In order of importance, mean (± SD) source proportions for the nestlings from this nest were 43 ± 11% terrestrial resources (rodents and deer), 30 ± 12% freshwater fish, 12 ± 9% flyingfish, 8 ± 6% seabirds, and 8 ± 6% marine fish. Mean (± SD) source proportions for the adults from this nest were 37 ± 9% terrestrial resources, 25 ± 10% freshwater fish, 17 ± 11% flyingfish, 11 ± 8% seabirds, and 11 ± 8% marine fish.

DISCUSSION

Our approach of combining identification of prey from nests with stable isotope analysis provided a comprehensive assessment of diet composition that yielded information on both prey diversity and ingested biomass for breeding Bald Eagles on the Channel Islands. Each of the dietary proxies used in this study has inherent biases that are important to consider when interpreting dietary patterns. When the 2 techniques are used in conjunction, however, the strengths of 1 particular approach supplement the weaknesses of the other. For example, identification of prey from nests may underestimate the consumption of small fish species by breeding eagles and their offspring, because the bones of small fish are difficult to collect without extensive excavation of the nest

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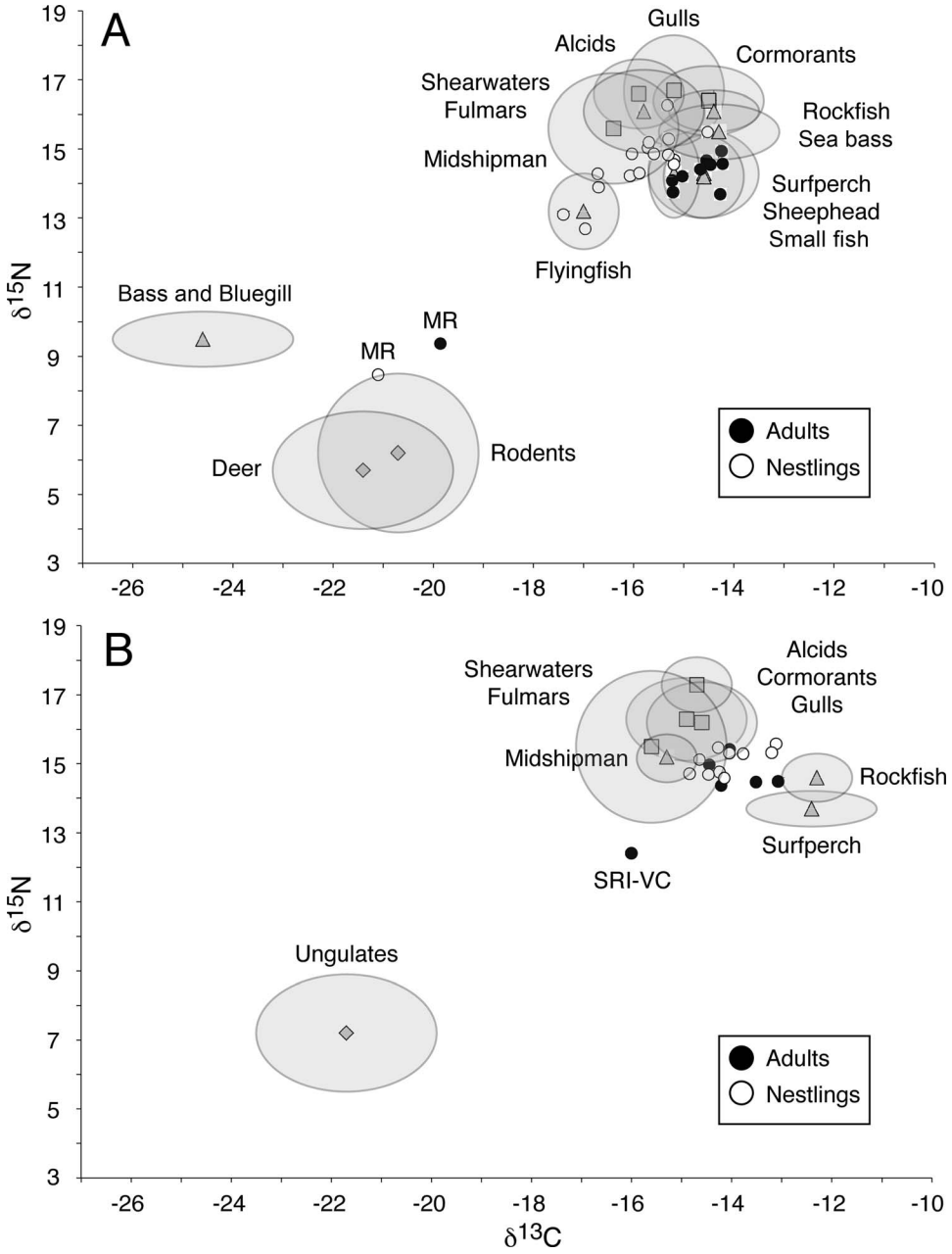


FIGURE 2. Bivariate plots of $\delta^{13}C$ vs. $\delta^{15}N$ of Bald Eagles (feathers) and their potential prey (bone collagen) collected from (**A**) Santa Catalina Island and (**B**) the Northern Channel Islands, California, USA; ellipses represent standard deviation. Small fish include species belonging to the Kyphosidae, Scrombridae, and Labridae (Tables 1 and 2). Bald Eagle adult feather isotope values have been corrected for trophic and tissue-specific discrimination by adding 1‰ to and subtracting 3‰ from measured feather $\delta^{13}C$ and $\delta^{15}N$ values, respectively. Bald Eagle nestling feather isotope values have been corrected for trophic and tissue-specific discrimination by adding 1‰ to and subtracting 2‰ from measured feather $\delta^{13}C$ and $\delta^{15}N$ values, respectively. For eagles that consumed a relatively high proportion of terrestrial resources, the nests of origin are labeled: Middle Ranch (MR) on Santa Catalina Island and Verde Canyon (SRI-VC) on Santa Rosa Island.

structure or may be completely digested by eagles with no traces left in the nest. Furthermore, while prey identification provides high-resolution information on the diversity of species consumed by eagles, this method does not take into account differences in the relative amounts of digestible biomass provided by different prey types. In contrast, stable isotope analysis provides a time-integrated measure of ingested biomass, but the method does not

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TABLE 3. $\delta^{13}C$ and $\delta^{15}N$ values (‰) of body feathers collected directly from Bald Eagle nestlings during annual banding activities or from adult primary and secondary feathers opportunistically collected from nests or adjacent perches on the Channel Islands, California, USA. Samples associated with band numbers are from nestlings. Isotope data for adults are mean values of 3 separate analyses corresponding to subsamples collected at the base, midshaft, and tip of a single primary or secondary feather; numbers in parentheses are standard deviation. An asterisk denotes that adult eagle feathers were collected from previously occupied nests that were in close vicinity to the active nests that pairs were using during our field campaigns in 2010–2011.

					Feather	
Band number	Sex	Island	Nest	Year	$\delta^{13}C$	$\delta^{15}N$
679-03445	M	Santa Catalina	Middle Ranch	2010	−22.1	10.5
679-03439	F	Santa Catalina	Pinnacle Rocks	2010	−16.2	16.7
679-03437	F	Santa Catalina	Rattlesnake	2010	−18.0	14.7
679-03438	M	Santa Catalina	Rattlesnake	2010	−17.1	16.2
679-04105	M	Santa Catalina	Rattlesnake	2011	−18.4	15.1
679-04104	F	Santa Catalina	Rattlesnake	2011	−17.7	15.9
679-03431	F	Santa Catalina	Seal Rocks	2010	−16.7	17.0
679-04103	M	Santa Catalina	Seal Rocks	2011	−16.3	18.3
679-04102	F	Santa Catalina	Seal Rocks	2011	−16.7	17.2
629-52435	M	Santa Catalina	Seal Rocks	2011	−15.5	17.5
679-03434	M	Santa Catalina	Two Harbors	2010	−16.9	16.3
679-03433	F	Santa Catalina	Two Harbors	2010	−16.2	16.6
679-04101	F	Santa Catalina	Two Harbors	2011	−16.3	17.3
679-03441	M	Santa Catalina	West End	2010	−16.6	16.9
679-03442	M	Santa Catalina	West End	2010	−16.3	16.8
679-04108	M	Santa Catalina	West End	2011	−17.7	16.3
679-04107	M	Santa Catalina	West End	2011	−17.0	16.9
679-03444	M	Santa Cruz	Cueva Valdez	2010	−15.2	16.8
679-04112	F	Santa Cruz	Cueva Valdez	2011	−15.6	17.1
679-03435	M	Santa Cruz	Pelican Harbor	2010	−15.8	16.7
679-03436	M	Santa Cruz	Pelican Harbor	2010	−15.5	16.7
679-04110	F	Santa Cruz	Pelican Harbor	2011	−14.8	17.3
679-03443	F	Santa Cruz	Sauces	2010	−15.2	16.6
679-04109	M	Santa Cruz	Sauces	2011	−15.0	17.3
679-03440	F	Santa Rosa	Lopez Canyon	2010	−14.1	17.6
679-03432	M	Santa Rosa	Verde Canyon	2010	−14.2	17.3
679-04111	M	Anacapa	Oak Canyon	2011	−15.3	17.5
—	—	Santa Catalina	Middle Ranch (Nest)	2010	−20.9 (0.2)	12.4 (0.7)
—	—	Santa Catalina	Seal Rocks (Perch)	2010	−16.2 (0.8)	16.8 (0.3)
—	—	Santa Catalina	Twin Rocks (Nest)	2010	−15.2 (0.3)	17.6 (0.2)
—	—	Santa Catalina	Seal Rocks (Nest)*	2010	−15.3 (0.3)	16.7 (0.1)
—	—	Santa Catalina	Pinnacle Rocks (Nest)	2010	−16.0 (0.3)	17.2 (0.4)
—	—	Santa Catalina	Rattlesnake (Perch)	2010	−16.2 (0.2)	17.1 (0.3)
—	—	Santa Catalina	Two Harbors (Perch)	2010	−15.5 (0.7)	17.6 (0.3)
—	—	Santa Catalina	Two Harbors (Nest)	2010	−15.7 (0.2)	17.4 (0.2)
—	—	Santa Catalina	West End (Perch)	2010	−15.2 (0.3)	17.9 (0.2)
—	—	Santa Catalina	West End (Nest)	2010	−15.5 (0.6)	17.7 (0.3)
—	—	Santa Cruz	Pelican Harbor (Nest)	2011	−15.0 (0.8)	18.4 (0.2)
—	—	Santa Cruz	Pelican Harbor (Nest)*	2011	−15.4 (0.1)	18.0 (0.3)
—	—	Santa Rosa	Lopez Canyon (Nest)	2010	−15.2 (0.6)	17.4 (0.1)
—	—	Santa Rosa	Verde Canyon (East Perch)	2010	−17.0 (0.6)	15.4 (0.7)
—	—	Santa Rosa	Verde Canyon (West Perch)	2010	−14.1 (0.5)	17.5 (0.2)
—	—	Santa Rosa	Verde Canyon (East Perch)	2010	−14.5 (0.5)	17.5 (0.3)

typically provide estimates of dietary composition at the species level. Stable isotopes measure ecological function and are thus particularly useful for determining the consumption of prey from different ecosystems (e.g., marine vs. terrestrial) or that occupy different trophic or habitat niches in the same ecosystem (e.g., marine fish and seabirds). Furthermore, the use of mixing models to convert stable isotope data into resource proportions can provide quantitative estimates of resource use. For situations in which the number of potential prey sources with distinct isotope values is much larger than the number of isotope systems (e.g., $\delta^{13}C$ and $\delta^{15}N$), Bayesian-based models do not always provide a clear quantitative picture of resource use (Phillips 2012). In our study, mixing models were run with 3 (NCI) or, at most, 5 (Catalina) isotopically distinct prey types, which yielded a

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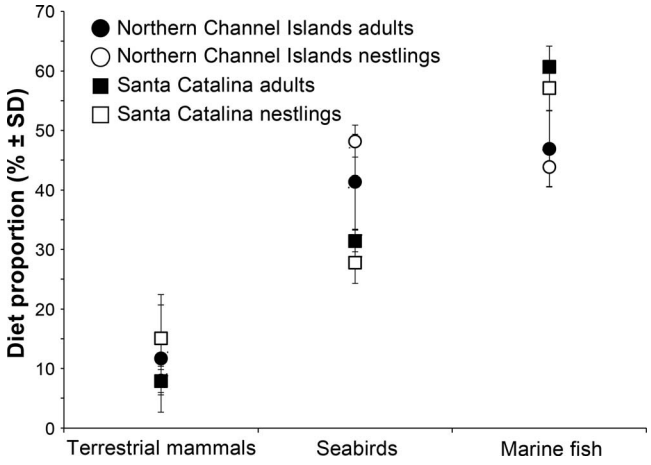


FIGURE 4. Results of Stable Isotope Analysis in R (SIAR) mixing model for Bald Eagle adult and nestling feathers collected from Santa Catalina Island (squares) and Northern Channel Islands (circles); error bars represent standard deviation. Results from the Middle Ranch nest on Santa Catalina Island are not included in this figure.

robust estimate of resource use that was consistent with results derived from the quantification of prey remains found in Bald Eagle nests.

Despite the different insights that identification of prey from nests and stable isotope analysis provide, both techniques revealed a consistent pattern of dietary differences between eagles on the NCI and Catalina. For example, results from isotope mixing models (Figure 3) showed that NCI eagles consumed a higher proportion of seabirds (~40–50%) than eagles from Catalina (~25–35%). The consumption of marine fish appeared to make up this difference, as mixing models showed that fish represented ~55–65% of eagle diets on Catalina and ~40–55% on the NCI. This pattern generally agreed with prey remains identified from nests (Table 1, Figure 1), with a higher proportion of seabirds in the NCI nests (54%) vs. Catalina nests (36%), and with marine fish more numerous in Catalina (55%) vs. NCI (43%) nests. On average, a seabird likely contains more digestible biomass than a fish, especially when considering the small fish species (e.g., flyingfish, wrasses) identified from Catalina nests. Not only did Catalina eagles consume a higher proportion of fish, but they also consumed a greater diversity of fish species than NCI eagles (Table 1, Figure 1). Based on the MNI, 3 families accounted for >90% of the fish identified from NCI nests. In contrast, we identified at least 5 individuals from each of 8 fish families from nests on Catalina.

A combination of natural and anthropogenic factors may be responsible for the observed dietary differences of eagles from the NCI and Catalina. First, recreational fishing may be an important factor in explaining the relatively high proportion and diversity of fish consumed by eagles on Catalina relative to those on the NCI. Recreational fishermen in southern California target many of the fish species identified from Catalina eagle nests. For example, Catalina nests contained California sheephead (*Semicossyphus pulcher*) and kelp bass (*Paralabrax* spp.), 2 nearshore species prized by recreational fisherman (Schroeder and Love 2002, Pacific States Marine Fisheries Commission 2014). These species were not identified in the 6 nests examined on the NCI. In addition, several species of small fish—wrasses, mackerel, and sea chub—were only identified in Catalina nests. Although it is possible that fish communities are more diverse and abundant in the waters off Catalina, there is less overall recreational fishing pressure off the NCI vs. Catalina for 2 reasons. First, larger portions of the coastal waters surrounding the NCI are designated marine protected areas within which commercial and recreational fishing is regulated or prohibited. Second, fewer recreational fishing vessels transport fisherman to the NCI from harbors in Ventura and Santa Barbara counties compared with the number that target Catalina from harbors elsewhere in southern California (https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=31344). Anecdotal observations by our team suggest that some eagles on Catalina have learned to associate recreational fishing boats with food and follow vessels to collect discards thrown overboard. This anthropogenic resource represents a subsidy that may confer benefits for Bald Eagles, but at the risk of entanglement in fishing gear.

Second, spatial differences in the relative availability of breeding seabirds between Catalina and the NCI may influence eagle diets. Since state and federal protection and the ban of harmful contaminants (e.g., organochlorides), the number of breeding seabirds has steadily increased in southern California over the past 4 decades (Table 4). Today, the Channel Islands host 16 species of resident breeding seabird, and at least as many seasonal migrants (e.g., loons, grebes, auklets, shearwaters, and fulmars) that breed in other parts of the North and South Pacific Ocean. Colonies of breeding seabirds are found on all 8 of the Channel Islands, but the largest and most productive colonies are on San Miguel, Santa Cruz, and Anacapa islands in the NCI (Table 4). Estimated numbers of breeding seabirds exceed 72,000 individuals on the NCI, compared with ~300 individuals on Catalina (Table 4).

Third, pinnipeds were only minor components of the eagle diet on both the NCI and Catalina (Table 1), thus they were excluded as a major prey type from isotope mixing models used to quantify diet composition. However, it is likely that free-flying eagles feed upon marine mammal carcasses when they are available and, as with other large prey (e.g., ungulates), strict use of identification of prey from nests to characterize use of

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TABLE 4. Estimates of population size and diversity of seabirds breeding on the Northern Channel Islands and Santa Catalina Island, California, USA. P = present and possibly breeding, E = breeding population extinct. Estimates are based on Carter et al. (1992) unless otherwise noted.

	Northern Channel Islands				
Species	San Miguel	Santa Rosa	Santa Cruz	Anacapa	Santa Catalina Island
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)	114				
Ashy Storm-Petrel (*Oceanodroma homochroa*)	1,354		323[a]	2[b]	<50[b]
Black Storm-Petrel (*Oceanodroma melania*)	P				
Brandt's Cormorant (*Phalacrocorax penicillatus*)	15,700	4,650	3,140	485[c]	E
Double-crested Cormorant (*Phalacrocorax auritus*)	552	16[c]	E	764[d]	E
Pelagic Cormorant (*Phalacrocorax pelagicus*)	691	1,162	460	328	
Brown Pelican (*Pelecanus occidentalis*)	204[e]		E	10,680	
Common Murre (*Uria aalge*)	70[f]–125[g]				
Pigeon Guillemot (*Cepphus columba*)	1,114	287	1,459	74	
Scripps's Murrelet (*Synthliboramphus scrippsi*)	100–600		200–600[h]	400–1,200[h]	100–200[i]
Cassin's Auklet (*Ptychoramphus aleuticus*)	11,584		736	4[j]	
Rhinoceros Auklet (*Cerorhinca monocerata*)	19[e]				
Tufted Puffin (*Fratercula cirrhata*)	4–10[f]				
Western Gull (*Larus occidentalis*)	1,892	170	1,236	10,274	156
Caspian Tern (*Hydroprogne caspia*)					8–10[a]
Total number of breeding species	13–14	5	7	9	4
Total number of breeding individuals	33,959	6,285	7,954	23,811	314–416

[a] USFWS (2009).
[b] H. R. Carter personal communication.
[c] Capitolo et al. (2006).
[d] Adkins and Roby (2010).
[e] Carter et al. (2008).
[f] Pandolfino et al. (2011).
[g] Adams and Felis (2011).
[h] Burkett et al. (2003).
[i] Whitworth et al. (2014).
[j] Whitworth et al. (2005).

this resource may be problematic because bones are heavy and difficult to transport back to nests.

Our results also showed that 3 eagles consumed a notable proportion of terrestrial resources. An adult feather collected from the Verde Canyon nest on Santa Rosa Island (Figure 2) had lower $\delta^{13}C$ and $\delta^{15}N$ values in comparison with feathers from other adults and nestlings from the NCI. Deer and elk were the only terrestrial prey found in nests on Santa Rosa Island, and our mixing model results showed that the adult from Verde Canyon consumed ~30% of this prey type, while ungulates were a negligible portion of the diet of other adults and nestlings on the NCI. Bald Eagle primary and secondary feathers are molted in the late summer and early fall, a time period that overlaps with the elk and deer hunt on Santa Rosa Island. Therefore, it is likely that this adult eagle from Verde Canyon was scavenging ungulate carcasses, which are typically left in place by trophy hunters on Santa Rosa Island. With the final transfer of Santa Rosa Island from private ownership to the National Park Service in 2012, all ungulates were removed from the island by 2013, and thus this source of prey is no longer available.

The 2 eagles that we sampled from the Middle Ranch nest on Catalina also had isotope values indicative of heavy reliance on terrestrial resources. Mixing model results (mean ± SD) showed that the Middle Ranch adult and nestling consumed 37 ± 9% and 43 ± 11% terrestrial mammals, respectively; freshwater fish were also a major prey source, accounting for ~25–30% of the diet of each individual. Identification of prey from nests and direct observation (P. Sharpe personal observation) showed that California ground squirrels (*Spermophilus beecheyi*) were the major terrestrial mammal species consumed by these 2 birds. The freshwater fish component was not surprising, as the Middle Ranch nest was adjacent to Thompson Reservoir, and Bald Eagles typically prefer fish when available (Stalmaster 1987). However, few studies have documented consistent depredation of a small mammal (<500 g) by a single individual or breeding pair of Bald Eagles (Mersmann et al. 1992, Grubb 1995). In addition to highlighting the diversity of prey consumed by Bald Eagles on the Channel Islands, this result shows that eagles are opportunistic generalists that can learn how to effectively hunt a wide variety of prey found in both marine and terrestrial habitats.

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Our previous studies of historic and prehistoric Bald Eagle diets on the Channel Islands (Collins et al. 2005, Erlandson et al. 2007, Newsome et al. 2010) provide an interesting comparison with the dietary patterns of the recently reestablished eagle population. As noted by Newsome et al. (2010) and confirmed by mixing models, many of the eagles from the NCI historically consumed a high proportion (25–75%) of domestic sheep, the only terrestrial resource that occurred in high abundance on the islands at the time. Several eagles that lived on the islands prehistorically (before the time of ranching on the islands) had isotope values that were indicative of terrestrial resource use; however, these birds were likely transient visitors to the islands from the mainland, a movement pattern noted for satellite-tracked reintroduced eagles (Sharpe 2007). For eagles in prehistoric times on the NCI that largely consumed marine resources, mixing model results showed that seabirds—not marine fish—were the dominant prey, comprising ~45% of the diet. This is a similar pattern to that observed among the reintroduced Bald Eagle population on the NCI. However, identification of prey from modern vs. historic nests suggests that the seabird species targeted by eagles has shifted over time. While the relative use of cormorants and auklets appears to be similar, nests of eagles reintroduced to the NCI contained a higher proportion of gulls (29% vs. 5%) but a lower proportion of ducks (5% vs. 13%) than identified from the historic eagle nest on San Miguel Island (Erlandson et al. 2007, Newsome et al. 2010). The temporal pattern in gull consumption is intriguing, given evidence that some North Pacific gull species have become more abundant over the past century, which may be associated with an increase in the use of anthropogenic resources (Blight et al. 2015a, 2015b).

Lastly, a comparison of modern and historic data suggests that the reintroduced Bald Eagle population has not yet reached carrying capacity, especially on the NCI. The Channel Islands currently support ~19 breeding pairs of Bald Eagles, nearly half of which are on Catalina. Early 20th century records suggest that at least 25 pairs nested across the archipelago in a single year, and ~50 nests were located by historic naturalists and egg collectors (P. W. Collins personal communication), although the same breeding pair may use different nests in the same general vicinity from year to year, probably inflating the number of nests. Locating and excavating additional historic nests across the Channel Islands will be required to examine regional patterns of the former population. Our team has excavated historic bald eagle nests on San Miguel, Santa Rosa, and San Nicolas islands, but given the estimated number of historic nests across the archipelago, more nest sites likely exist and await discovery.

Our understanding of ecological baselines for animal communities is confounded by centuries, if not millennia, of human harvest, compounded by habitat alteration and ecosystem change (Pauly 1998, Jackson et al. 2001, Pinnegar and Englehard 2008). Information on contaminant levels (Bond et al. 2015), genetic diversity (Pinsky et al. 2010, Alter et al. 2012), dietary preferences (Newsome et al. 2010, Wiley et al. 2013, Blight et al. 2015b), and the size and location of breeding sites (Newsome et al. 2007b) in the past and present can indicate how modern and ancient anthropogenic activities have affected animal populations, and may help to set reference targets for the management of animal populations in coastal ecosystems. When combined with previously published information on historic and ancient populations of Bald Eagles in the Channel Islands archipelago (Collins et al. 2005, Erlandson et al. 2007, Newsome et al. 2010), the dietary data for the reintroduced population presented here provides a unique perspective on the ecological plasticity of this apex coastal predator in response to both spatial and long-term temporal (centuries to millennia) variation in prey availability.

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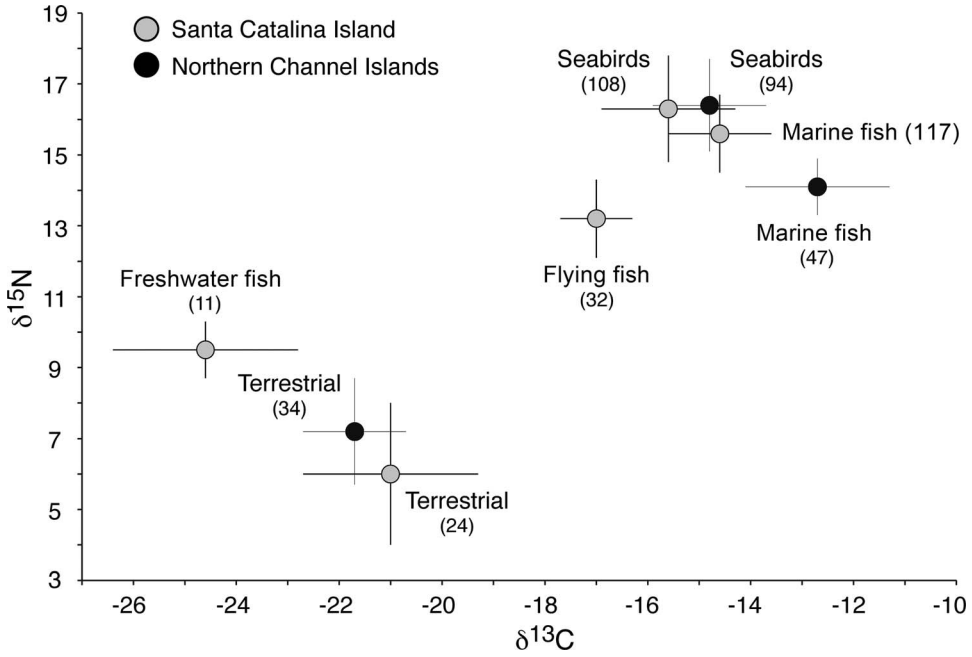
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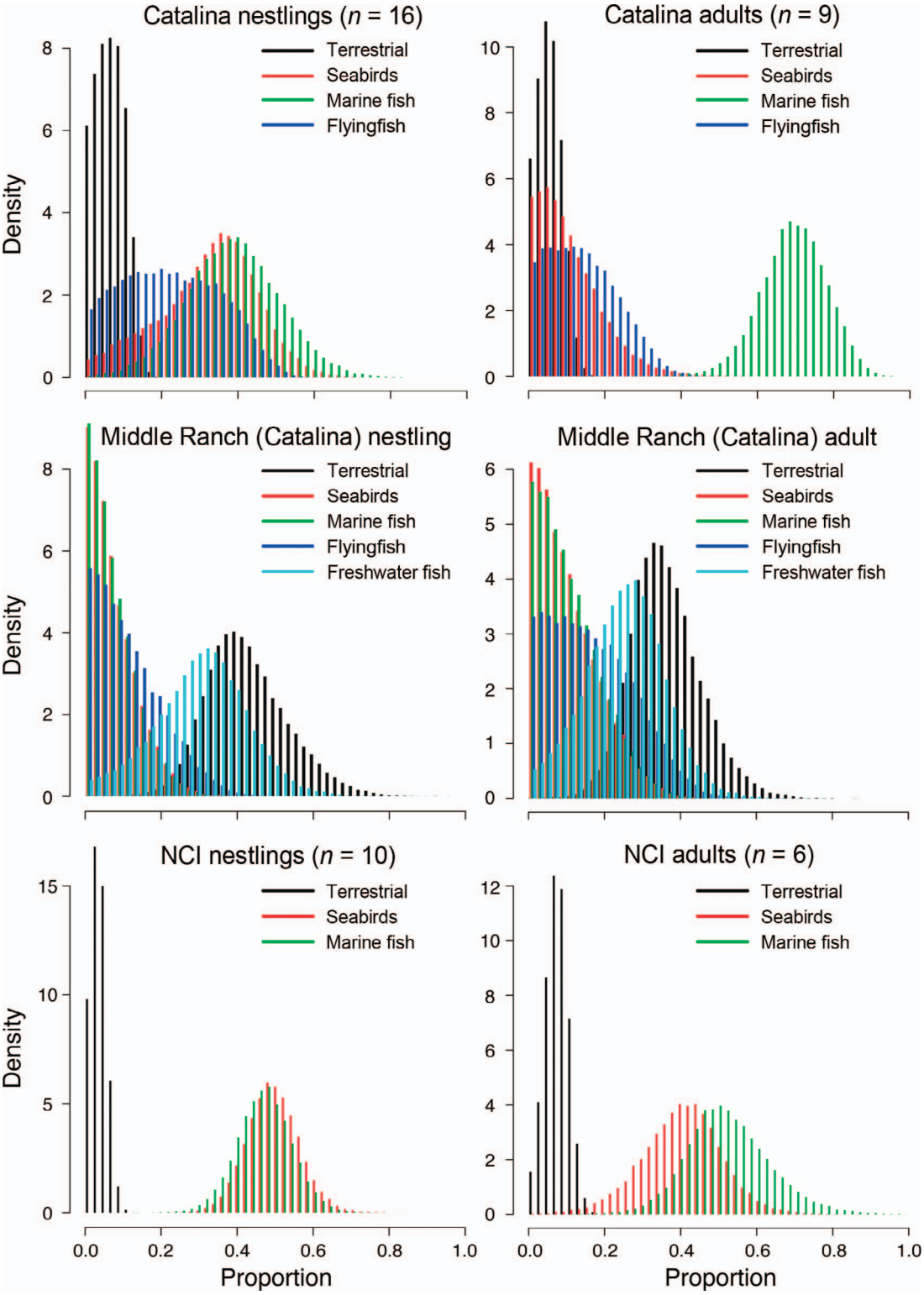
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APPENDIX FIGURE 3. Mean bone collagen $\delta^{13}C$ and $\delta^{15}N$ values for major prey types of Bald Eagles on Santa Catalina Island and the Northern Channel Islands, California, USA, used in Stable Isotope Analysis in R (SIAR) mixing models; error bars represent standard deviation, and sample sizes are noted in parentheses.

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APPENDIX FIGURE 5. Posterior frequency histograms of source proportions of the major prey types used in the Stable Isotope Analysis in R (SIAR) mixing models for Bald Eagle nestlings and adults from Santa Catalina Island (Catalina) and the Northern Channel Islands (NCI), California, USA. Results are grouped by island and locality, and sample sizes are noted in parentheses. The Bald Eagle nestling (middle left panel) and adult (middle right panel) from the Middle Ranch nest were run separately in a mixing model that included 5 major prey types.

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