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Factors affecting the distribution and abundance of autumn vagrant warblers in northwestern California and southern Oregon

C. John Ralph [1, 2] , **Jared Wolfe** [Corresp. 1, 2, 3]

[1] Pacific Southwest Research Station, USDA Forest Service, Arcata, California, United States
[2] Klamath Bird Observatory, Ashland, Oregon, United States
[3] School of Forest Resources and Environmental Sciences, Michigan Technological University, Houghton, Michigan, United States

Corresponding Author: Jared Wolfe
Email address: jdw@klamathbird.org

Birds found outside their typical range, or vagrants, have fascinated naturalists for decades. Despite broad interest in vagrancy, few attempts have been made to statistically examine the explanatory variables potentially responsible for the phenomenon. In this study, we used multiple linear regression to model the occurrence of 28 rare warbler species (family Parulidae) in autumn in northern California and southern Oregon as a function of migration distance, continental population size, distance, and bearing to both closest breeding population and breeding population center. In addition to our predictive model, we used capture data from the California coast to 300 km inland to examine relationships between the presence of vagrant warblers, regional warbler species richness and age class distribution. Our study yielded three important results: (1) vagrancy is strongly correlated with larger North American population size and secondarily by longer migration distance; (2) vagrants are more common at some coastal sites; and (3) where young birds are over-represented, vagrants tend to occur – such as on the coast and at far inland sites. Of the many explanations of rare and vagrant individuals, we feel that the most likely is that these birds represent the ends of the distributions of a normal curve of migration direction, bringing some few migrants to locations out of their normal migratory range as vagrants. We also examine the underrepresented species that, according to our model, are overdue for being recorded in our study area.

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C. John Ralph[1,2] and Jared D. Wolfe[1,2,3]

[1]USDA Forest Service, Pacific Southwest Research Station, Arcata, California 95521

[2]Klamath Bird Observatory, Ashland, Oregon 97520

[3] School of Forest Resources and Environmental Sciences, Michigan Technological University, Houghton, Michigan 49931

* Corresponding author: jdwolfe@mtu.edu

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Keywords: migration, vagrant birds, California, Oregon, age ratio, warbler, Parulidae

INTRODUCTION

Bird observers have been long fascinated by the appearance of rare or out of range birds, and the opportunity to speculate on the causes of such vagrants.

> *"The erratic wanderings of migratory birds, resulting in their appearance in countries far removed from their accustomed haunts, and off the routes followed to reach them, are in many cases to be attributed to their failure, from some cause or other, to inherit unimpaired this all-important faculty of unconscious orientation. The incentive to migrate, it must be admitted, is strong within them, or they would never occur in places so remote from the domains of their respective species."* WILLIAM EAGLE CLARKE (1912)

Coastal areas, such as northwestern California, are noted for their frequency of rare birds. The conspicuous nature of coastal vagrancy led Grinnell (1922) to predict that all species in North America would eventually turn up in California. We are, in investigating the significance and explorations of the phenomenon of vagrancy, tempted to hypothesize that the exceptions in normal migration routes that vagrants exemplify could illuminate rules that most migrants follow. Because vagrancy generates excitement among bird observers, many prominent naturalists have speculated on the mechanisms responsible for the occurrence of rare birds: weather, geography, migration overshoots, deviant directional tendencies (right time but wrong direction -- misorientation), mirror-image migration, and reversed direction migration (Rabøl 1976, Burger et al. 1980, McLaren 1981, DeSante 1983a, Montalti et al. 1999, Newton

2008). Despite interest in publishing theories regarding the causes of vagrancy, relatively few attempts (*see* Hampton 1997) have been made to statistically examine the influence of multiple explanatory factors on the prevalence of vagrancy at the landscape scale.

Similar to vagrancy, a disproportionately high number of young birds (less than six months old) are regularly observed during fall migration along California's northwest coast. The preponderance of young birds found in coastal regions was termed the 'coastal effect' by Ralph (1978, 1981). It was suggested that the coastal effect is a manifestation of misoriented young nocturnal migrants being forced to return to land at sunrise after traveling above the ocean, resulting in more young birds near coastal areas (Ralph 1978). Similarities between coastal vagrancy and the coastal effect are striking, where young and vagrant birds appear to be relatively more common near the coast, and may simply reflect the misorientation of both young of many species and vagrant birds. More specifically, if young birds are more prone to becoming lost (similar to a lost vagrant bird), than there will be a correlation between the abundance of young and vagrant birds at geographic boundaries, such as oceans and deserts, that prevent passage across the landscape. Furthermore, if vagrant species are more abundant along coastlines, then coastal communities should be more species rich when compared to their inland counterparts. In this study, we conducted three analyses to explore factors influencing the presence and richness of vagrant and young birds across northern California and southern Oregon.

First, we used vagrant warbler records from northern California to examine the relative importance of six explanatory factors in illuminating the likely causes of vagrancy in New World warblers (Parulidae). Based on these findings we provided a method of predicting which warbler species have likely been missed by observers. Second, we used capture data from northern California and southern Oregon to determine if vagrancy asymmetrically influenced warbler species richness across the landscape. Third, we used capture data to test the prediction that young and vagrant warblers probably represent lost birds subject to the vagaries of geography, and their abundances are, therefore, statistically correlated across the landscape.

METHODS

Vagrancy is a site-specific phenomenon, as one area's common bird is another's rare vagrant, or out of range species, so we limited our study to two overlapping study areas. The first study area is delineated by the 28 bird banding stations used in this study (from our network of 239 banding stations known as the Klamath Bird Monitoring Network; Alexander and Ralph 2004) in northern California and southern Oregon (Fig. 1). The second study area is based on the meticulous compilation of all available records from all observers in northwestern California by Harris (2006) that includes the western half of Siskiyou County, all of Del Norte, Humboldt, and Trinity counties, and the northern half of Mendocino County. From this, we retrieved fall sightings (September through November) of all vagrant warbler species (Table 1) documented from 1970 through 2006.

We defined a vagrant as a species that was detected at least once, and with a maximum of a total of 500 records, over a 36 year period (Harris 2006) . We felt that this was a useful number that differentiated relatively rare migrant birds from vagrant species that are occurring outside their normal range. For example, we did not consider the Palm Warbler (*Setophaga palmarum*) a vagrant, but a regular, yet rare, migrant with some 1,100 fall records. We found that 28 warbler species could be classified as vagrants because of their rarity (Table 1).

For our predictive model, the response variable was a log transformation (to normalize the distribution) of the total number of individuals of each vagrant species detected during fall migration from Harris (2006). So, for example, Black-throated Blue Warbler had 51 and Blue-winged Warbler had three individuals documented during fall migration in northern California; each of these values represented a single datum. We used six explanatory variables to explain fall vagrant warbler sightings: migration distance, size of the North American breeding population (log), distance to closest population (log), bearing to closest population, distance to population center (log), and bearing to population center. Migration distance class was calculated by the number of degrees latitude between the breeding and wintering ranges using BirdLife range maps (http://www.birdlife.org/datazone/species). Similarly, we calculated distance to closest population, bearing to closest population, distance to population center, and bearing to population center. Distance estimates were to the nearest 100 km, from the combined center of the four counties of our study area to the center of each species' breeding range. North American population estimates were taken from Rich et al. (2004).

We formulated 16 competitive multiple-linear regression models (Table 2), including a null (no explanatory variables) and global model (all explanatory variables) using program R (R Core Team 2012). Models were formulated *a priori* based on a combination of explanatory variables we believed most influenced vagrancy. Next, we ranked each model by using Akaike Information Criterion values corrected for small sample sizes (AICc) where the top model was selected if it was at least two AICc values lower, and/or had fewer parameters relative to the next most competitive model (Arnold 2010). We also included 95% confidence intervals with explanatory variable beta estimates and adjusted R^2 with each model to provide additional information regarding how well each model performed and fit the data. Once the top model was selected, we used covariate data from ten other warbler species (Table 1) that had not yet been documented in the study area, but were possible candidates for future vagrant status (Tropical Parula, Olive Warbler, Painted Redstart, Pine Warbler, Grace's Warbler, Red-faced Warbler, Swainson's Warbler, Golden-cheeked Warbler, Louisiana Waterthrush and Kirtland's Warbler), to predict which species was most likely to occur in northern California.

Next, we used capture and banding data from 28 stations across southern Oregon and northern California, representing eight geographic regions, to explore relationships between location and warbler species occurrences. Each of the stations had at least a total of 10,000 mist-net hours of banding data during fall migration, and for convenience were subjectively grouped into regions based on empirical criteria of distance to the coast, latitude, altitude, and habitat (Fig. 1) (Table 3). Most nets at all stations were amongst riparian vegetation that has a higher capture rate than nearby habitat, whether it is oak woodland or dense coniferous forest.

To estimate the number of species of both all warblers and vagrant warblers, we generated Chao1 estimates of total and vagrant warbler richness, using program EstimateS (Colwell 2005), at each banding station to examine the influence of vagrancy on warbler richness across southern Oregon and northern California. The Chao1 diversity index uses the ratio of species detected only once or twice to generate predicted estimates of species richness. The formula used for Chao1 estimates are based on Chao (1987) where $S_{observations}$ refers to total number of species observed in all samples pooled and F_1 and F_2 refer to species detected only once or twice:

$$\hat{S}_{chao1} = S_{observations} + \frac{F1^2}{F2^2}$$

Finally, we used the same Klamath banding dataset (described above) to test the hypothesis that the proportion of young birds and vagrant bird abundances are correlated across the landscape (DeSante 1973, Ralph 1981). To examine this hypothetical relationship, we performed a simple linear regression to examine the correlation between the percent of all warbler species pooled that were young, and the abundance of vagrant warblers captured per 1000 net-hours across the eight geographic regions in southern Oregon and northern California during fall migration.

RESULTS

Factors Affecting the Occurrence of Vagrants

Using the number of fall records of the 28 vagrant species as a response variable (Table 1), we investigated combinations of six likely explanatory variables. We selected the top model based on being within 2 AICc values of the lowest value, while having the fewest number of parameters (Arnold 2010). Based on these criteria, we selected North American population size as the most competitive explanatory variable explaining vagrancy in northern California (Table 2). Specifically, we found that vagrancy was positively correlated with the North American breeding population (Fig. 2), indicating that the larger the species' breeding population, the more likely it is to occur in northern California as a vagrant (β=0.622; SE=0.087; CI=[0.45,0.79]). Based on our model selection criteria (Arnold 2010), our second most competitive model yielded the lowest AICc value and contained migration distance as an additional positively correlated explanatory variable (β=1.246; SE=0.285; CI=[0.69,1.80]), suggesting that the farther migrants travel, the more prone they are to vagrancy. Together, the two most competitive models encompassed 64% of the AICc Weight, and each explained 56% of the variance. The next most competitive model had the second lowest AICc value and included two additional parameters where beta confidence intervals did not overlap zero, suggesting species with nearer breeding populations (β=-2.154; SE=0.84; CI=[-0.504, -3.804]) coupled with more direct bearings to breeding range centers (β=-0.036; SE=-0.018; CI=[-0.0003, -0.072]) exhibited more vagrancy. This latter model contained two other additional explanatory variables where beta estimate confidence intervals overlapped zero and were therefore deemed not significant:

distance to center of breeding population (β=1.246; SE=0.285; CI=[0.69,1.80]), and bearing to center of breeding population (β=1.246; SE=0.285; CI=[0.69,1.80]).

Species Recorded Less or More Often than Expected

We detected a strong linear relationship between the number of fall records for the 28 species and the size of their North American breeding population, with most falling near the regression line (Fig. 2). The possibly instructive exceptions include those underrepresented, seen much less often than the population size would predict, with their values below the regression line (that is, the largest negative residuals), including Cerulean Warbler and Mourning Warbler. Conversely, "overrepresented" species tending to be recorded more often than would be predicted (the largest positive residuals) included Prairie Warbler, Virginia's Warbler, Black-and-White Warbler, and Black-throated Blue Warbler.

We included the predicted number of records of ten species of warblers that have never been recorded in northern California to identify what species, according to our model, should have been detected (Fig. 2). Painted Redstart, Swainson's Warbler, Red-faced Warbler, Louisiana Waterthrush would have been predicted to be detected fewer than three times, but Grace's Warbler had ~10 predicted records and Pine Warbler possibly more than 50 records. The other four species with no records had populations of less than 40,000 and would have a low probability of occurring in northwest California.

Influence of Vagrancy on Warbler Species Richness

When comparing the number of warbler species at the 11 stations that had at least one vagrant species occurring (Fig. 3), we found that vagrant warblers at the HOME station (in the Coastal Region) accounted for 9 of the 26 estimated species (36%). This was our highest ratio of vagrant to total species; this finding indicates that vagrancy strongly influenced total warbler richness at our most species-rich site. Conversely, vagrants at inland stations generally accounted for a smaller proportion of total warbler species richness, with 17 stations having none or relatively few vagrants. These species-poor stations could be located just inland from the coast, such as 7% at the RED2 station in the Redwood Region, only 4.5 km from the coast. At the much farther inland sites, however, the estimated proportion of vagrants rose again sharply to 19% at CABN and 20% at ODES on the western shore of Upper Klamath Lake in the Upper Klamath Region (Fig. 3).

Associations between Young Birds of all species and Vagrants

A high proportion of young birds at a station usually indicates that the station is on a coastline (the "coastal effect" of Ralph 1978, 1981). To examine if both young birds in general, and vagrant abundances, are similarly over-represented in certain regions across the study area, we employed linear regression using percent of young (all non-vagrant warblers pooled) as the response and vagrant warbler abundance captured across the regions as the explanatory variables. Our analysis found a moderately-significant relationship between the percent of young birds and the abundance of vagrant warblers captured across the eight geographic regions. Specifically, while beta estimate confidence intervals slightly overlapped zero (β=0.299;

SE=0.163; CI=[0.02,0.62]), associated adjusted R^2 values were high, where vagrant records explained 25% of the variance in non-vagrant age ratios. Thus, areas with higher proportions of young warblers tended to have more vagrant warblers. As expected, the region with both the highest proportion of young and the highest proportion of vagrant warblers was the coastal region (Fig. 4, Table 3).

DISCUSSION

Our analysis revealed three major insights: (1) vagrancy is largely driven by large population size and migratory behaviors – species with more individuals, and species that move longer-distances, both increase the likelihood of being detected outside a species' normal range. This is a logical confirmation and extension of other studies (e.g., Stake 2012); (2) vagrancy drives warbler richness in some coastal sites and does not affect warbler richness at other, more inland sites; and (3) stations where young warblers account for a higher proportion of total captures, vagrant warblers also tend to occur – such as on the coast. Our findings suggest that young and vagrant birds have something in common: they both may be more prone to navigational mistakes, and therefore more often occur on the coast, an inherently dangerous place for these nocturnal migrants.

In an early analysis of California warblers, DeBenedictis (1971) also presented some subjective evidence that continental population size accounted for some variation in abundance of vagrants in California. He also suggested involvement of the angle of deviation from normal migration routes needed to reach California. He found no evidence that length of migration route had any relationship. By contrast, DeSante (1983b) suggested that on the Farallon Islands, some 30 km offshore, the abundance of vagrant warblers might be related to their respective commonness in North America. Another analysis by Hampton (1997) examining patterns of vagrancy relied on a linear model to explore factors that may have influenced the occurrence of 84 rare species throughout coastal and central northern California . Of the six explanatory variables included in a linear model, he found support for the following variables in explaining the occurrence of vagrants: westernmost longitude of a species' breeding range, taxonomic status, distance to the nearest edge of the breeding range, and easterly migratory route. Interestingly, unlike our findings, Hampton found little support for population size. Differences in Hampton's (1997) and our findings may reflect statistical methodologies, that is we ranked a series of competitive models using AICc, while Hampton explored a single model. Our study area and taxonomic unit, wood warblers in northern California, was also much smaller relative to Hampton's that included all vagrant landbirds across much of the state.

Interestingly, we found four warbler species with no records in northern California (Harris 2006) that, according to our model, should have been recorded at least once. Two species would be predicted to have a single individual Louisiana Waterthrush and Red-faced Warbler; but two others would be much more abundant: Grace's Warbler with three records and the Pine Warbler with four records predicted. However, the facultative migratory behavior of the Pine Warbler may be partly responsible for the overestimation of their potential occurrence in our study area (F. Moore, pers. comm.). Assuming that our predictive model is robust, both Grace's and Pine warbler could have been missed by observers because they are more accurate in their navigation, or because of identification problems, as both species are relatively cryptic. Pine Warbler resembles the somewhat more common Blackpoll Warbler, and other species, such as the Orange-crowned Warbler (*Oreothlypis celata*). Grace's Warbler is a southwestern species, and may be confused with immature Townsend's Warbler (*Setophaga townsendi*), a common species in the study area. Several other species appear to be relatively under-detected, and below the trend line. These are generally either cryptic or hard to detect (e.g., Mourning Warbler, underrepresented by almost an order of magnitude, and Connecticut Warbler both of which are likely confused with the common migrant MacGillivray's Warbler (*Geothlypis tolmiei*). In addition to appearing similar to MacGillivray's Warbler, Connecticut Warblers prefers thick vegetation near the ground making them inherently difficult to find. According to our model, other underrepresented vagrants include Ovenbird and Cerulean Warbler, both of which may be challenging to detect because Ovenbirds prefer forested understories and the Cerulean Warbler frequents forest canopies – an arduous stratum to look for birds in the often-towering trees of the north coast. By contrast, overrepresented species, seen relatively more often than their population size would indicate, are typically conspicuous, or easily identified species, such as Black-and-white Warbler, Prairie Warbler, Chestnut-sided Warbler, American Redstart, and Black-throated Blue Warbler. It is also possible that, in addition to being conspicuous, these overrepresented species may be more prone to misorientation or have produced more young during the years of this study, relative to other species, thereby increasing the probability of young vagrants being detected on the coast.

A high proportion of young birds on the Pacific coast, the “coastal effect” (Ralph 1978, 1981) is suggested to be primarily due to misorientation of the relatively naïve young individuals at the edge of their migratory flyway. Several hundred kilometers farther inland is another periphery of many migrant species’ routes, the eastern portion of our study area, where the habitat is less salubrious, and on the eastern edge of a major habitat type, the coniferous Cascade Mountains, and on the western edge of the relatively inhospitable Great Basin. In this portion of our study area, we found an increase in the number of vagrants, but did not find a concomitant high proportion of young. The increase of vagrants here along the western shore of Upper Klamath Lake may be related to this shoreline, acting as a “coast” analogous to the shore of the Pacific Ocean. In addition, it is quite possible that young on the coast may be due to one phenomenon, and the occurrence of vagrants might also be related to this, but not entirely. For example, Austin (1971) found that migrants which breed east of the Rockies typically occur three weeks or so later in migration than migration dates in the east. A high percentage of these lost vagrants are immature. He suggested that they were transported westward, by airflows from east across the southwestern states, that could have played a role, as well as misorientation. However, DeSante (1973) clearly found that vagrant wood warblers in California occurred on time, relative to their average timing on their normal migration route.

While today’s vagrant might be tomorrow’s model citizen, destined to become a colonizer and perhaps an established resident, as Grinnell (1922) asserted, most vagrants might be viewed as failed colonization attempts. Newton (2008:267-299) summarized quite well the various explanations of the causes of vagrancy put forward over the past century or so. They include:

normal dispersal over long distances, population growth or expansion, drift by winds, migration overshoots, deviant directional tendencies (right time but wrong direction), mirror-image migration, and reversed direction migration. While all explanations probably play a role and explain the occurrence of some vagrant individuals, we address the latter three explanations as they likely involve the vast majority of landbirds. The mirror-image misorientation theory, originally developed by DeSante (1973), and lucidly described by Diamond (1982), proposed that vagrants are misoriented by confusion of right and left in relating an inherited migration direction to a compass reference direction. Mirror-image misorientation theory accounts for observations made by DeSante (1983a) that in certain situations large-angle misorientations seem more frequent than small or intermediate deviations from the normal migration course (Alerstam 1990). Misorientation by the wind has long been suggested as a cause of accidentals (e.g. Austin 1971), but Thorup, et al. (2012) found differently, as the authors used radio telemetry to track individual migratory flights of several species of songbirds from the Faroe Islands, approximately halfway between Norway and Iceland, far west of their normal migration route. Birds with expected easterly and south-easterly migration direction departed westwards out over the Atlantic Ocean, indicating that these birds are actively flying in the ‘‘wrong’’ direction and that their occurrence is not caused by wind drift. However, on Attu Island, in the Aleutian Islands off Alaska, Hameed et al. (2009) found statistical evidence that the occurrence of spring Asian vagrants on this North Pacific island were correlated with storm winds from the west.

In helpful comments on our analysis, DeSante (pers. comm.) suggested that none of our proposed explanatory variables really captures the essence of either simple misorientation or mirror-image misorientation in determining the abundance of vagrants, because they do not include information on the normal fall migration routes of the various species. For example, American Redstart and Black-and-white Warbler may be more abundant than predicted from source populations alone because they winter commonly in southern Baja California, much farther west than other species with similar breeding ranges, and thus require much smaller degrees of simple misorientation from their normal fall migration route to reach northern California than species that do not winter as far west. Similarly, he notes, Prairie, Black-throated Blue and Blackpoll warblers may be more abundant than predicted because the strong easterly components of their normal fall migration routes facilitate the occurrences in California of mirror-image vagrants.

We would advance that perhaps a more parsimonious explanation of the phenomenon, and certainly part of some of the mechanisms listed above, is that these vagrants represent the ends of the distributions of a normal curve of the migration direction of the species, thus bringing some few migrants to unaccustomed locations. As to the other explanations that have been advanced, as Newton (2008:299) notes “possible bias in observer coverage throws doubt on some apparent examples of mirror-image and reversed-direction migration, and neither mechanism can be considered as proven or disproven.” Our explanation of misorientation of young along the coast as being the result of deviant directional tendencies remains well-demonstrated (e.g. Ralph 1978). Hence, it remains quite likely that the probability of an individual migrant suffering from deviant directional tendencies increases with population size, leading to our documented correlation between the abundance of vagrant warblers and total population size.

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Figure 1

Map of the study area

Location of capture stations across the study area, and further divided into biogeographical regions based on similarities of distance to the coast, altitude, and habitat.

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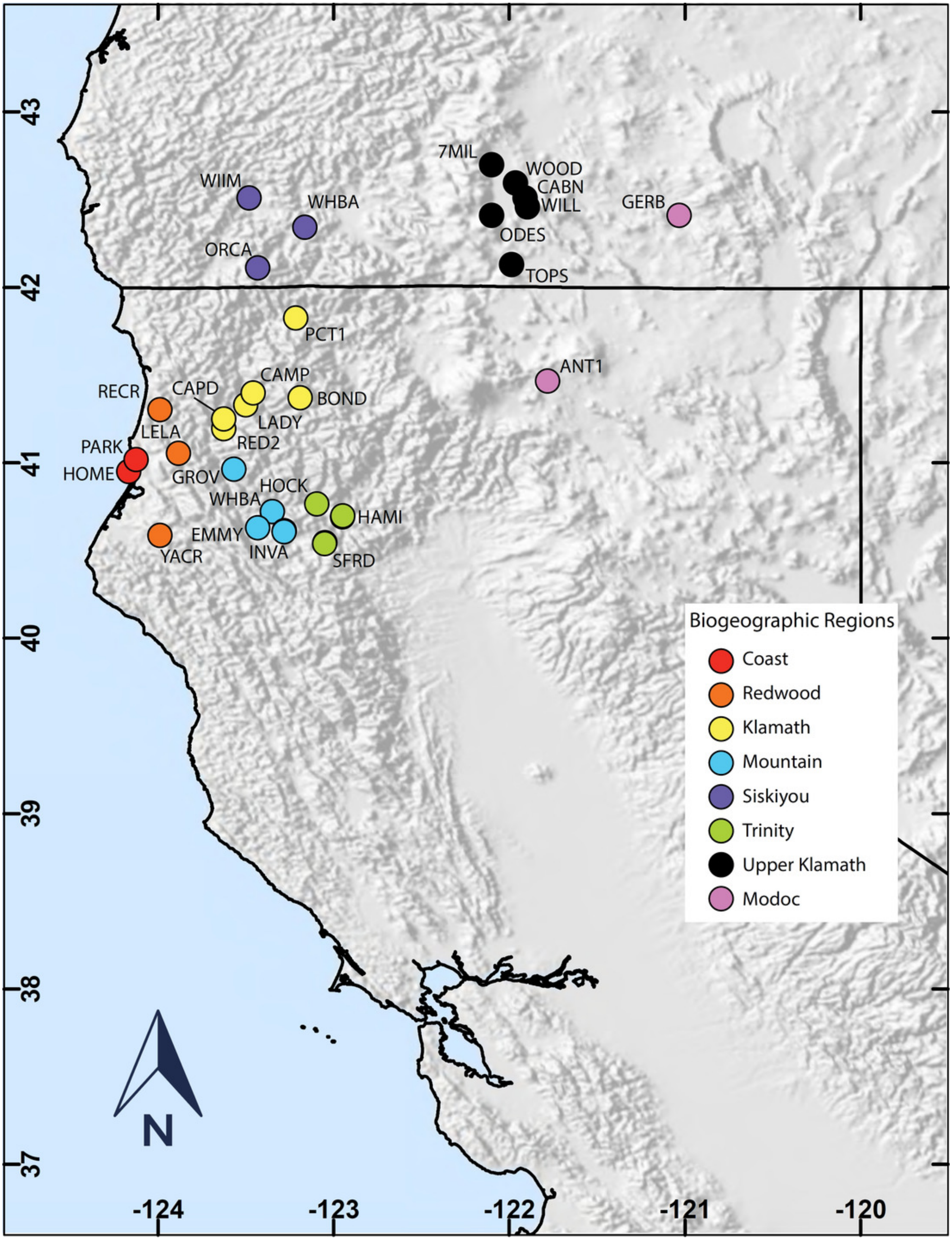
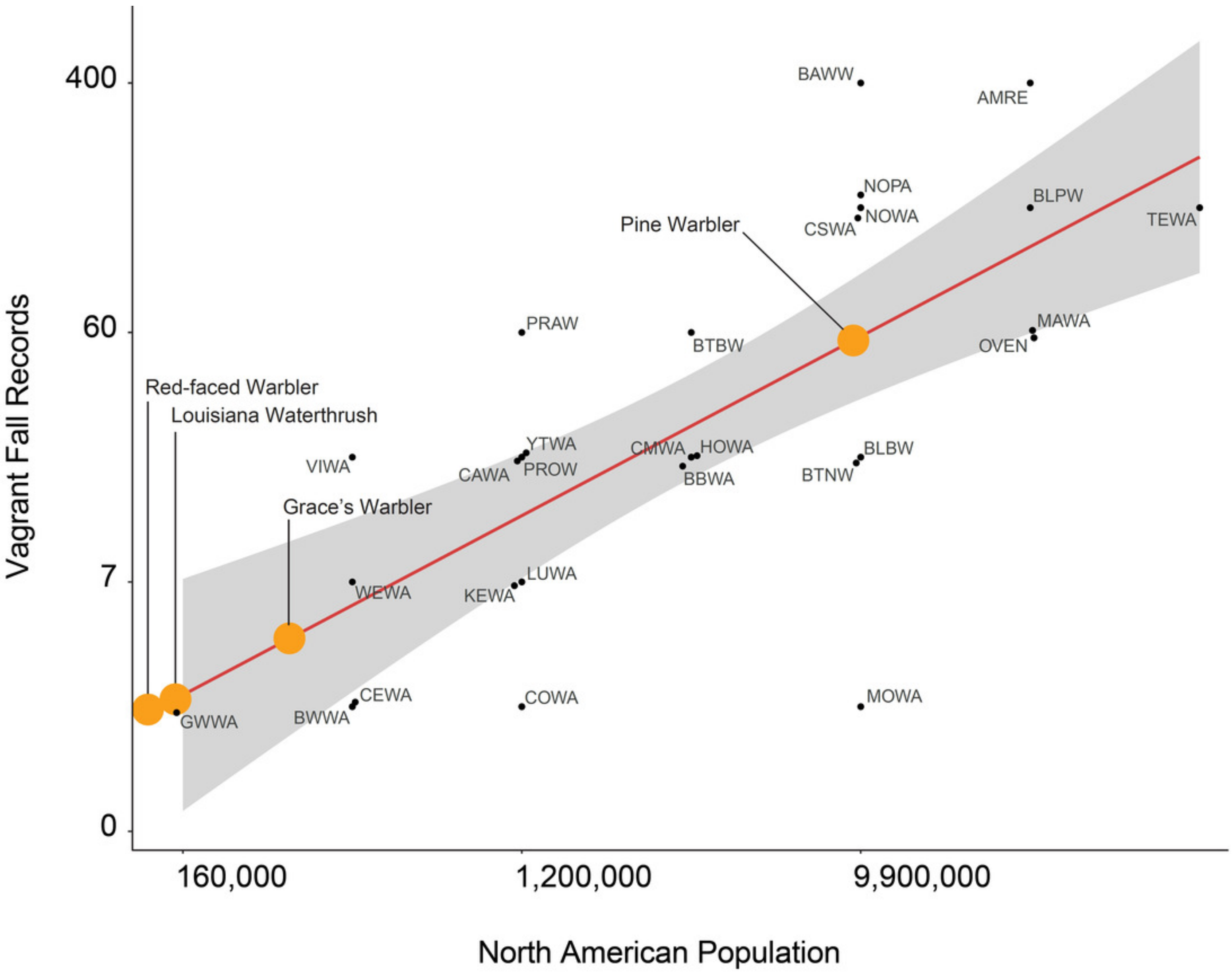

7MIL
WOOD
CABN
WILL
ODES
TOPS
GERB
WIIM
WHBA
ORCA
PCT1
ANT1
CAMP
CAPD
BOND
RECR
LADY
LELA
RED2
PARK
HOME
GROV
HOCK
WHBA
HAMI
EMMY
INVA
SFRD
YACR
Biogeographic Regions
Coast
Redwood
Klamath
Mountain
Siskiyou
Trinity
Upper Klamath
Modoc
N
43
42
41
40
39
38
37
-124
-123
-122
-121
-120

Figure 2

Visualization of the top model predicting vagrant warbler occurence

Visualization of our top model demonstrating a positive correlation between North American population size and number of vagrants detected in northern California (taken from Harris 2006). Each four-letter code represents the AOU short-hand abbreviation for each warbler species. Orange marks indicate predicted occurrence of yet unrecorded vagrant warbler species in northern California; six unrecorded vagrant warbler species have small populations and thus do not appear in this figure as they would fall below, or well below, an observation of a single individual predicted: Tropical Parula, Painted Redstart, Olive Warbler, Swainson's Warbler, Golden-cheeked Warbler, and Kirtland's Warbler.



400
60
7
0
Vagrant Fall Records
160,000
1,200,000
9,900,000
North American Population
BAWW
AMRE
NOPA
BLPW
NOWA
CSWA
TEWA
Pine Warbler
PRAW
BTBW
MAWA
OVEN
Red-faced Warbler
Louisiana Waterthrush
YTWA
CMWA
HOWA
BLBW
VIWA
CAWA
PROW
BBWA
BTNW
Grace's Warbler
WEWA
LUWA
KEWA
CEWA
COWA
MOWA
BWWA
GWWA

Figure 3

Diversity estimates of warblers at banding stations

Estimated number of vagrant warbler species (upper) in the 11 stations with at least one species of vagrant recorded and estimated total warbler species (lower) at all 28 bird capture stations, with standard error bars, and grouped (colored) by the eight biogeographic regions in southern Oregon and northern California between 1992 and 2008.

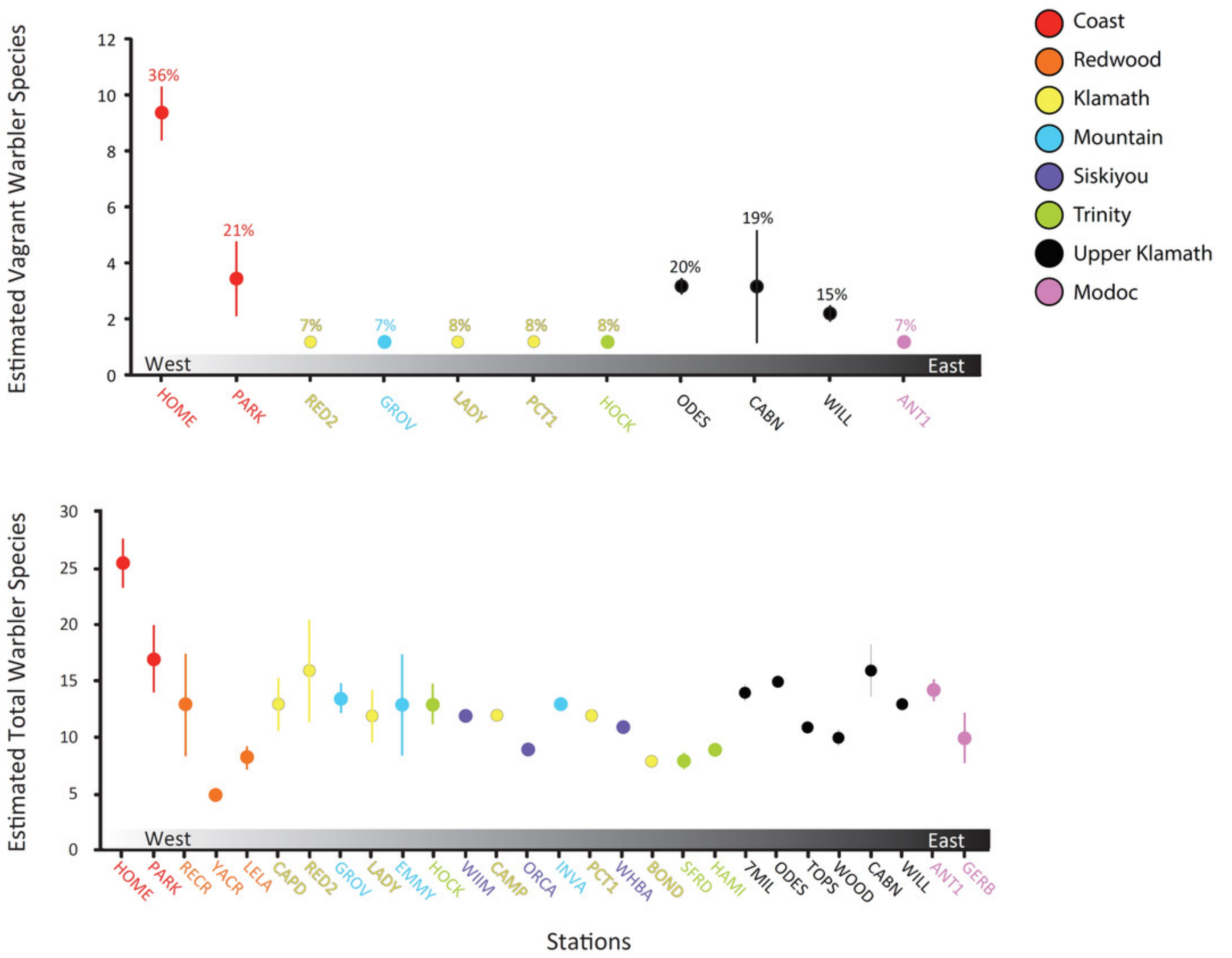


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Figure 4

Relationship between vagrant and young warblers

Visualization of our linear regression examining the relationship between the number of vagrant warblers and proportion of non-vagrant warbler age ratios (hatching year [HY]/ after-hatching year [AHY]). Data were collected from 28 bird capture stations, across eight

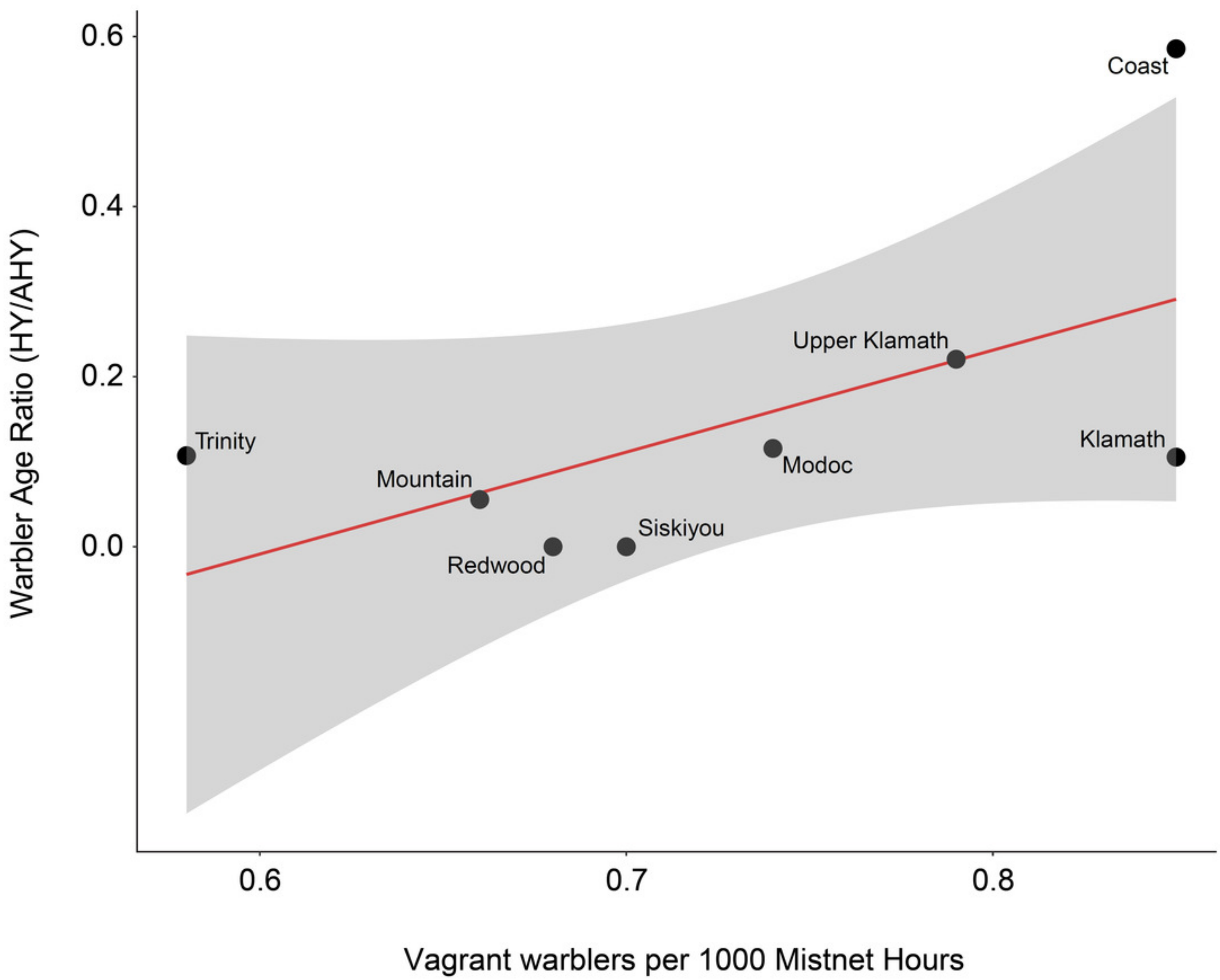

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Table 1(on next page)

Variables used in predictive vagrant warbler models

Variables used to predict autumn vagrancy of warblers (recorded fewer than 500 times) in northwestern California (from Harris 2006)

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Species	Migratory Distance	North American Population	Fall Records	Distance to Closest Breeding Range (km)	Bearing to Closest	Distance to Center of Population (km)	Bearing to Center
American Redstart (AMRE)	31.38	25,000,000	343	400	41	1800	63
Bay-breasted Warbler (BBWA)	39.22	3,000,000	25	1000	7	1700	56
Black-and-white Warbler (BAWW)	34.09	14,000,000	247	800	32	2000	70
Blackburnian Warbler (BLBW)	46.08	5,900,000	27	1000	31	2200	68
Blackpoll Warbler (BLPW)	53.28	20,000,000	208	800	358	1700	37
Black-throated Blue Warbler (BTBW)	23.83	2,000,000	51	1700	62	2400	66
Black-throated Green Warbler (BTNW)	30.34	10,000,000	14	900	19	2000	70
Blue-winged Warbler (BWWA)	34.09	390,000	3	1500	84	2200	80
Canada Warbler (CAWA)	47.88	1,400,000	14	900	20	2000	66
Cape May Warbler (CMWA)	36.39	3,000,000	18	900	12	1700	55
Cerulean Warbler (CEWA)	41.44	560,000	1	1400	82	2200	81
Chestnut-sided Warbler (CSWA)	29.51	9,400,000	134	1000	25	2200	65
Connecticut Warbler (COWA)	53.21	1,200,000	3	1000	25	1500	48
Golden-cheeked Warbler (GCWA)	16.01	21,000	0	1600	109	1600	72
Golden-winged Warbler (GWWA)	33.32	210,000	3	1300	47	2200	72
Grace's Warbler (GRWA)	11.84	1,000,000	0	600	127	1800	114
Hooded Warbler (HOWA)	18.80	4,000,000	27	1500	82	2200	85
Kentucky Warbler (KEWA)	19.87	1,100,000	4	1500	92	2000	87
Kirtland's Warbler (KIWA)	20.62	2,100	0	2000	72	2000	132
Louisiana Waterthrush (LOWA)	20.97	260,000	0	1500	94	2100	110
Lucy's Warbler (LUWA)	11.57	900,000	5	600	128	1000	126
Magnolia Warbler (MAWA)	33.92	30,000,000	75	700	11	1800	57
Mourning Warbler (MOWA)	43.44	7,000,000	2	900	20	2000	66
Northern Parula (NOPA)	19.88	7,300,000	89	1000	90	1800	84
Northern Waterthrush (NOWA)	40.57	13,000,000	101	400	58	1500	39
Olive Warbler (OLWA)	0.00	17,000	0	900	119	1800	129
Ovenbird (OVEN)	26.05	24,000,000	34	800	56	1900	74
Painted Redstart (PARE)	8.82	40,000	0	700	124	1800	94
Pine Warbler (PIWA)	12.13	11,000,000	0	1500	56	2200	78
Prairie Warbler (PRAW)	15.69	1,400,000	53	1500	91	2100	86

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Prothonotary Warbler (PROW)	20.39	1,800,000	25	1500	101	2100	89
Red-faced Warbler (RFWA)	0.00	110,000	0	700	124	1100	126
Swainson's Warbler (SWWA)	12.24	84,000	0	1700	108	2100	84
Tennessee Warbler (TEWA)	42.47	60,000,000	144	700	33	1700	51
Tropical Parula (TRPA)	31.38	3,000	0	1200	131	3800	128
Virginia's Warbler (VIWA)	18.53	400,000	15	300	119	800	107
Worm-eating Warbler (WEWA)	19.43	700,000	10	1500	82	2200	86
Yellow-throated Warbler (YTWA)	16.71	1,600,000	20	1500	82	2200	88

Table 2(on next page)

Predicitive model rankings

Candidate models used to predict warbler vagrancy in northern California and associated differences in corrected AIC values (ΔAICc), AICc weights (w_{AICc}), model deviance, number of parameters (*k*), and adjusted R^2 values. The most competitive model was selected if it was at least two AICc values lower, and/or had fewer parameters relative to the next most competitive model (Arnold 2010).

Model	ΔAICc	w_{AICc}	Deviance	*k*	adj. R^2
Migratory Distance + North American Population	0.00	0.44	25.92	3	0.56
Migratory Distance + North American Population + Distance to Closest Breeding Population + Bearing to Closest Breeding Population + Distance to Center of Breeding Population + Bearing to Center of Breeding Population	0.68	0.31	16.20	7	0.67
North American Population	1.53	0.20	30.19	2	0.50
North American Population + Distance to Closest Breeding Population + Bearing to Closest Breeding Population	5.08	0.03	27.94	4	0.50
North American Population + Distance to Center of Breeding Population + Bearing to Center of Breeding Population	6.87	0.01	29.78	4	0.47
Migratory Distance + Distance to Center of Breeding Population + Bearing to Center of Breeding Population	13.84	0.00	38.19	4	0.32
Distance to Closest Breeding Populatiom + Bearing to Closest Breeding Population + Distance to Center of Breeding Population + Bearing to Center of Breeding Population	15.04	0.00	35.47	5	0.34
Distance to Closest Breeding Population	16.71	0.00	51.93	2	0.15
Bearing to Center of Breeding Population	19.00	0.00	56.34	2	0.07
Distance to Closest Breeding Population + Bearing to Closest Breeding Population	19.13	0.00	51.34	3	0.12
null	19.72	0.00	63.25	1	n/a
Distance to Center of Breeding Population + Bearing to Center of Breeding Population	21.26	0.00	55.40	3	0.05
Migratory Distance + Distance to Closest Breeding Population + Bearing to Closest Breeding Population	21.76	0.00	50.67	4	0.10
Bearing to Closest Breeding Population	21.95	0.00	62.61	2	0.00
Distance to Center of Breeding Population	22.20	0.00	63.17	2	0.00
Migratory Distance	22.21	0.00	63.19	2	0.00

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Table 3(on next page)

Capture summaries of vagrant and non-vagrant warblers

Number captured (n), percent young (%HY), percent unknown age (%Unk) of vagrant and non-vagrant warblers detected during fall migration at each capture station (site), grouped by biogeographic region (region), between 1992 and 2008.

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Region	Site	mistnet hours	Non-vagrant *n*	Non-vagrant %HY	Non-vagrant %Unk	Vagrant *n*	Vagrant %HY	Vagrant %Unk
Coast	PARK	14748	446	0.84	0.25	5	0.8	0
Coast	HOME	51845	2494	0.85	0.19	34	0.88	0
Coast Total		**66593**	**2940**	**0.85**	**0.22**	**39**	**0.84**	**0**
Redwood	RECR	3809	110	0.58	0.08	0	n/a	n/a
Redwood	LELA	1495	44	0.65	0.02	0	n/a	n/a
Redwood	YACR	2769	70	0.68	0.06	0	n/a	n/a
Redwood Total		**8072**	**70**	**0.68**	**0.06**	**0**	**n/a**	**n/a**
Klamath	CAPD	9739	453	0.87	0.09	0	n/a	n/a
Klamath	RED2	4258	287	0.78	0.08	2	1	0
Klamath	CAMP	5944	352	0.83	0.05	0	n/a	n/a
Klamath	LADY	6564	553	0.77	0.07	1	1	0
Klamath	BOND	658	54	0.79	0.04	0	n/a	n/a
Klamath	PCT1	10775	735	0.84	0.09	1	1	0
Klamath Total		**37939**	**2434**	**0.85**	**0.07**	**4**	**1**	**0**
Mountain	EMMY	2449	69	0.55	0.04	0	n/a	n/a
Mountain	INVA	7364	1134	0.65	0.1	0	n/a	n/a
Mountain	GROV	8219	1021	0.79	0.12	1	1	0
Mountain Total		**18031**	**2224**	**0.66**	**0.09**	**1**	**1**	**0**
Siskiyou	ORCA	2790	300	0.83	0.07	0	n/a	n/a
Siskiyou	WHBA	3808	73	0.54	0.03	0	n/a	n/a
Siskiyou	WIIM	16467	2529	0.74	0.04	0	n/a	n/a
Siskiyou Total		**23065**	**2902**	**0.7**	**0.05**	**0**	**n/a**	**n/a**
Trinity	HOCK	3395	213	0.53	0.38	1	0	1
Trinity	SFRD	3564	98	0.49	0.27	0	n/a	n/a
Trinity	HAMI	2381	168	0.74	0.14	0	n/a	n/a
Trinity Total		**9340**	**479**	**0.58**	**0.26**	**1**	**0**	**1**
Upper Klamath	TOPS	4307	491	0.75	0.08	0	n/a	n/a
Upper Klamath	ODES	5605	1073	0.81	0.1	5	0.2	0
Upper Klamath	CABN	13803	3958	0.83	0.13	2	1	0

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Upper Klamath	7MIL	6569	446	0.84	0.25	0	n/a	n/a
Upper Klamath	WOOD	5130	1229	0.83	0.11	0	n/a	n/a
Upper Klamath	WILL	5394	1434	0.68	0.15	2	1	0
Upper Klamath Total		**40809**	**8631**	**0.79**	**0.14**	**9**	**0.73**	**0**
Modoc	ANT1	4152	1640	0.75	0.1	1	0	0
Modoc	GERB	4496	431	0.74	0.12	0	n/a	n/a
Modoc Total		**8648**	**2071**	**0.74**	**0.11**	**1**	**0**	**0**
Total		**203851**	**21751**	**0.73**	**0.13**	**55**	**0.6**	**0.15**