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

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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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23 Birds found outside their typical range, or vagrants, have fascinated naturalists for decades. 24 Despite broad interest in vagrancy, few attempts have been made to statistically examine the 25 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) 26 27 in autumn in northern California and southern Oregon as a function of migration distance, 28 continental population size, distance, and bearing to both closest breeding population and 29 breeding population center. In addition to our predictive model, we used capture data from the 30 California coast to 300 km inland to examine relationships between the presence of vagrant 31 warblers, regional warbler species richness and age class distribution. Our study yielded three 32 important results: (1) vagrancy is strongly correlated with larger North American population 33 size and secondarily by longer migration distance; (2) vagrants are more common at some 34 coastal sites; and (3) where young birds are over-represented, vagrants tend to occur – such as 35 on the coast and at far inland sites. Of the many explanations of rare and vagrant individuals, 36 we feel that the most likely is that these birds represent the ends of the distributions of a 37 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, 38 according to our model, are overdue for being recorded in our study area. 39

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

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45 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.
- 48

49	"The erratic wanderings of migratory birds, resulting in their appearance in
50	countries far removed from their accustomed haunts, and off the routes followed
51	to reach them, are in many cases to be attributed to their failure, from some
52	cause or other, to inherit unimpaired this all-important faculty of unconscious
53	orientation. The incentive to migrate, it must be admitted, is strong within them,
54	or they would never occur in places so remote from the domains of their
55	respective species." WILLIAM EAGLE CLARKE (1912)
56	

57 Coastal areas, such as northwestern California, are noted for their frequency of rare birds. The 58 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 59 60 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 61 62 follow. Because vagrancy generates excitement among bird observers, many prominent 63 naturalists have speculated on the mechanisms responsible for the occurrence of rare birds: weather, geography, migration overshoots, deviant directional tendencies (right time but 64 65 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 66

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.

70

71 Similar to vagrancy, a disproportionately high number of young birds (less than six months old) 72 are regularly observed during fall migration along California's northwest coast. The 73 preponderance of young birds found in coastal regions was termed the 'coastal effect' by Ralph 74 (1978, 1981). It was suggested that the coastal effect is a manifestation of misoriented young 75 nocturnal migrants being forced to return to land at sunrise after traveling above the ocean, 76 resulting in more young birds near coastal areas (Ralph 1978). Similarities between coastal 77 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 78 79 young of many species and vagrant birds. More specifically, if young birds are more prone to 80 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, 81 82 that prevent passage across the landscape. Furthermore, if vagrant species are more abundant 83 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 84 85 influencing the presence and richness of vagrant and young birds across northern California and 86 southern Oregon.

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88 First, we used vagrant warbler records from northern California to examine the relative 89 importance of six explanatory factors in illuminating the likely causes of vagrancy in New World 90 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 91 92 northern California and southern Oregon to determine if vagrancy asymmetrically influenced 93 warbler species richness across the landscape. Third, we used capture data to test the 94 prediction that young and vagrant warblers probably represent lost birds subject to the 95 vagaries of geography, and their abundances are, therefore, statistically correlated across the landscape. 96

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98 METHODS

Vagrancy is a site-specific phenomenon, as one area's common bird is another's rare vagrant, 99 100 or out of range species, so we limited our study to two overlapping study areas. The first study 101 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 102 103 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 104 Harris (2006) that includes the western half of Siskiyou County, all of Del Norte, Humboldt, and 105 106 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 107 108 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).

115

116 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 117 118 migration from Harris (2006). So, for example, Black-throated Blue Warbler had 51 and Blue-119 winged Warbler had three individuals documented during fall migration in northern California; 120 each of these values represented a single datum. We used six explanatory variables to explain 121 fall vagrant warbler sightings: migration distance, size of the North American breeding 122 population (log), distance to closest population (log), bearing to closest population, distance to 123 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 124 125 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 126 127 bearing to population center. Distance estimates were to the nearest 100 km, from the 128 combined center of the four counties of our study area to the center of each species' breeding 129 range. North American population estimates were taken from Rich et al. (2004).

130 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 131 132 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 133 Information Criterion values corrected for small sample sizes (AICc) where the top model was 134 selected if it was at least two AICc values lower, and/or had fewer parameters relative to the 135 next most competitive model (Arnold 2010). We also included 95% confidence intervals with 136 137 explanatory variable beta estimates and adjusted R^2 with each model to provide additional 138 information regarding how well each model performed and fit the data. Once the top model 139 was selected, we used covariate data from ten other warbler species (Table 1) that had not yet 140 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 141 142 Warbler, Swainson's Warbler, Golden-cheeked Warbler, Louisiana Waterthrush and Kirtland's 143 Warbler), to predict which species was most likely to occur in northern California.

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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.

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153 To estimate the number of species of both all warblers and vagrant warblers, we generated 154 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 155 156 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 157 used for Chao1 estimates are based on Chao (1987) where Sobservations refers to total number of 158 159 species observed in all samples pooled and F₁ and F₂ refer to species detected only once or 160 twice:

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

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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.

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174 **RESULTS**

175 Factors Affecting the Occurrence of Vagrants

Using the number of fall records of the 28 vagrant species as a response variable (Table 1), we 176 investigated combinations of six likely explanatory variables. We selected the top model based 177 on being within 2 AICc values of the lowest value, while having the fewest number of 178 179 parameters (Arnold 2010). Based on these criteria, we selected North American population size 180 as the most competitive explanatory variable explaining vagrancy in northern California (Table 181 2). Specifically, we found that vagrancy was positively correlated with the North American 182 breeding population (Fig. 2), indicating that the larger the species' breeding population, the 183 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 184 yielded the lowest AICc value and contained migration distance as an additional positively 185 186 correlated explanatory variable (β =1.246; SE=0.285; CI=[0.69,1.80]), suggesting that the farther 187 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 188 189 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 190 191 nearer breeding populations (β =-2.154; SE=0.84; CI=[-0.504, -3.804]) coupled with more direct 192 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 193 estimate confidence intervals overlapped zero and were therefore deemed not significant: 194

- 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]).
- 197

198 Species Recorded Less or More Often than Expected

We detected a strong linear relationship between the number of fall records for the 28 speciesand the size of their North American breeding population, with most falling near the regression

201 line (Fig. 2). The possibly instructive exceptions include those underrepresented, seen much

202 less often than the population size would predict, with their values below the regression line

203 (that is, the largest negative residuals), including Cerulean Warbler and Mourning Warbler.

204 Conversely, "overrepresented" species tending to be recorded more often than would be

205 predicted (the largest positive residuals) included Prairie Warbler, Virginia's Warbler, Black-and-

206 White Warbler, and Black-throated Blue Warbler.

207

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.

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217 Influence of Vagrancy on Warbler Species Richness

218 When comparing the number of warbler species at the 11 stations that had at least one vagrant 219 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 220 vagrant to total species; this finding indicates that vagrancy strongly influenced total warbler 221 222 richness at our most species-rich site. Conversely, vagrants at inland stations generally 223 accounted for a smaller proportion of total warbler species richness, with 17 stations having 224 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. 225 226 At the much farther inland sites, however, the estimated proportion of vagrants rose again 227 sharply to 19% at CABN and 20% at ODES on the western shore of Upper Klamath Lake in the Upper Klamath Region (Fig. 3). 228

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230 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 231 (the "coastal effect" of Ralph 1978, 1981). To examine if both young birds in general, and 232 233 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 234 235 response and vagrant warbler abundance captured across the regions as the explanatory 236 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 237 regions. Specifically, while beta estimate confidence intervals slightly overlapped zero (β =0.299; 238

SE=0.163; CI=[0.02,0.62]), associated adjusted R² 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).

244

245 **DISCUSSION**

246 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-247 248 distances, both increase the likelihood of being detected outside a species' normal range. This 249 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 250 251 inland sites; and (3) stations where young warblers account for a higher proportion of total 252 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 253 navigational mistakes, and therefore more often occur on the coast, an inherently dangerous 254 place for these nocturnal migrants. 255

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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

261 route had any relationship. By contrast, DeSante (1983b) suggested that on the Farallon 262 Islands, some 30 km offshore, the abundance of vagrant warblers might be related to their 263 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 264 occurrence of 84 rare species throughout coastal and central northern California . Of the six 265 explanatory variables included in a linear model, he found support for the following variables in 266 267 explaining the occurrence of vagrants: westernmost longitude of a species' breeding range, 268 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. 269 270 Differences in Hampton's (1997) and our findings may reflect statistical methodologies, that is 271 we ranked a series of competitive models using AICc, while Hampton explored a single model. 272 Our study area and taxonomic unit, wood warblers in northern California, was also much 273 smaller relative to Hampton's that included all vagrant landbirds across much of the state. 274 Interestingly, we found four warbler species with no records in northern California (Harris 2006) 275 that, according to our model, should have been recorded at least once. Two species would be 276 277 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 278 279 Warbler with four records predicted. However, the facultative migratory behavior of the Pine 280 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 281 and Pine warbler could have been missed by observers because they are more accurate in their 282

283 navigation, or because of identification problems, as both species are relatively cryptic. Pine 284 Warbler resembles the somewhat more common Blackpoll Warbler, and other species, such as 285 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 286 species in the study area. Several other species appear to be relatively under-detected, and 287 below the trend line. These are generally either cryptic or hard to detect (e.g., Mourning 288 Warbler, underrepresented by almost an order of magnitude, and Connecticut Warbler both of 289 290 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 291 292 vegetation near the ground making them inherently difficult to find. According to our model, 293 other underrepresented vagrants include Ovenbird and Cerulean Warbler, both of which may be challenging to detect because Ovenbirds prefer forested understories and the Cerulean 294 295 Warbler frequents forest canopies – an arduous stratum to look for birds in the often-towering 296 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 297 as Black-and-white Warbler, Prairie Warbler, Chestnut-sided Warbler, American Redstart, and 298 299 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 300 301 during the years of this study, relative to other species, thereby increasing the probability of 302 young vagrants being detected on the coast.

303

304 A high proportion of young birds on the Pacific coast, the "coastal effect" (Ralph 1978, 1981) is 305 suggested to be primarily due to misorientation of the relatively naïve young individuals at the 306 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 307 salubrious, and on the eastern edge of a major habitat type, the coniferous Cascade Mountains, 308 and on the western edge of the relatively inhospitable Great Basin. In this portion of our study 309 area, we found an increase in the number of vagrants, but did not find a concomitant high 310 311 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 312 313 Ocean. In addition, it is quite possible that young on the coast may be due to one phenomenon, 314 and the occurrence of vagrants might also be related to this, but not entirely. For example, 315 Austin (1971) found that migrants which breed east of the Rockies typically occur three weeks 316 or so later in migration than migration dates in the east. A high percentage of these lost 317 vagrants are immature. He suggested that they were transported westward, by airflows from 318 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 319 320 time, relative to their average timing on their normal migration route.

321

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:

326 normal dispersal over long distances, population growth or expansion, drift by winds, migration 327 overshoots, deviant directional tendencies (right time but wrong direction), mirror-image 328 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 329 they likely involve the vast majority of landbirds. The mirror-image misorientation theory, 330 originally developed by DeSante (1973), and lucidly described by Diamond (1982), proposed 331 332 that vagrants are misoriented by confusion of right and left in relating an inherited migration 333 direction to a compass reference direction. Mirror-image misorientation theory accounts for observations made by DeSante (1983a) that in certain situations large-angle misorientations 334 335 seem more frequent than small or intermediate deviations from the normal migration course 336 (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 337 338 telemetry to track individual migratory flights of several species of songbirds from the Faroe 339 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 340 out over the Atlantic Ocean, indicating that these birds are actively flying in the "wrong" 341 342 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 343 344 of spring Asian vagrants on this North Pacific island were correlated with storm winds from the 345 west.

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347 In helpful comments on our analysis, DeSante (pers. comm.) suggested that none of our 348 proposed explanatory variables really captures the essence of either simple misorientation or 349 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, 350 American Redstart and Black-and-white Warbler may be more abundant than predicted from 351 source populations alone because they winter commonly in southern Baja California, much 352 353 farther west than other species with similar breeding ranges, and thus require much smaller 354 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-355 356 throated Blue and Blackpoll warblers may be more abundant than predicted because the strong 357 easterly components of their normal fall migration routes facilitate the occurrences in California 358 of mirror-image vagrants.

359

360 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 361 ends of the distributions of a normal curve of the migration direction of the species, thus 362 363 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 364 365 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 366 young along the coast as being the result of deviant directional tendencies remains well-367 demonstrated (e.g. Ralph 1978). Hence, it remains quite likely that the probability of an 368

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.

372

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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.



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.

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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.



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]/ afterhatching year [AHY]). Data were collected from 28 bird capture stations, across eight



Vagrant warblers per 1000 Mistnet Hours

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)

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

Pee	10 Preprints		NOT PE	ER-REVIEWED	0		
Prothenotony Warbler (PPOW)	20.20	1 800 000	25	1500	101	2100	00
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 (Δ AICc), AICc weights (w_{AICc}), model deviance, number of parameters (k), and adjusted R² 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	WAICc	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 +	0.68	0.31	16.20	7	0.67
Bearing to Center of Breeding Population					
North American Population	1.53	0.20	30.19	2	0.50
North American Population + Distance to Closest Breeding Population + Bearing to Closest	E 00	0.02	27.04	4	0 5 0
Breeding Population	5.08	0.05	27.94	4	0.50
North American Population + Distance to Center of Breeding Population + Bearing to Center	6 97	0.01	20.79	Λ	0.47
of Breeding Population	0.87	0.01	29.70	4	0.47
Migratory Distance + Distance to Center of Breeding Population + Bearing to Center of	12 0/	0.00	29 10	Λ	0 22
Breeding Population	13.04	0.00	56.19	4	0.52
Distance to Closest Breeding Populatiom + Bearing to Closest Breeding Population +	15 04	0.00	25 /17	5	0.34
Distance to Center of Breeding Population + Bearing to Center of Breeding Population	13.04	0.00	55.47	J	0.54
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	21 76	0.00	F0 67	4	0 10
Population	21.70	0.00	50.07	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

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.

		_	Non-vagr	ant		Vagrant		
Region	Site	mistnet hours	n	%HY	%Unk	п	%HY	%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

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

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