GENE FLOW IN SCRUB JAYS: FREQUENCY AND DIRECTION OF MOVEMENT[1]

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Abstract. Based on strong differences in plumage coloration between coastal California (*californica* subspecies group) and Great Basin (*woodhouseii* subspecies group) populations of Scrub Jays (*Aphelocoma coerulescens*), museum specimens representing gene flow between the two forms are identified. A total of 27 examples of apparent genetic exchange between two forms (individuals of one subspecies group taken within the range of the other) is documented. Immigration rates are on the order of one per hundred or one per thousand individuals, a rate sufficient to prevent differentiation by genetic drift alone if effective population sizes are in the range of 100–550 individuals. Gene flow east-to-west across the Mojave Desert is two to seven times stronger than west-to-east movement. This directional bias has theoretical implications because an important assumption (symmetry of gene flow patterns) of most theoretical treatments of the effects of gene flow is violated. If effective population sizes are comparable in the two forms, then the bias in gene flow should lead to an overall greater rate of differentiation in the genetically more isolated *woodhouseii* populations.

Key words: Gene flow; population differentiation; dispersal; Corvidae; Scrub Jay.

INTRODUCTION

The importance of gene flow in preventing differentiation of populations has been debated extensively in recent decades (Mayr 1963; Ehrlich and Raven 1969; Endler 1973, 1977; Slatkin 1987). Some authors argue that gene flow is a critical constraint on the differentiation of populations (e.g., Mayr 1963), whereas others emphasize the importance of factors such as natural selection (e.g., Ehrlich and Raven 1969). The issue hinges critically on the overall magnitude of gene flow as it relates to historical factors, current ecological factors, and population structure and dynamics.

Actual measurements of levels of gene flow in natural populations, however, are relatively rare. Modes of estimation include direct techniques, such as studies of dispersal distances of marked individuals, and indirect techniques, such as the use of Wright's *F*-statistics or frequencies of "private" alleles (reviewed in Slatkin 1985b) derived from biochemical studies. When both approaches have been applied to the same species, they often produce very different results (Slatkin

1985a): indirect estimates are generally considerably higher than direct estimates, perhaps due to the effects of rare, long-distance dispersal, or due to the nonequilibrium nature of many natural populations. Nevertheless, the species for which both types of estimates exist are few, making evaluation of these techniques difficult.

Scrub Jays (*Aphelocoma coerulescens*) range from northern Oregon to southern Mexico, and from central Texas to the Pacific Ocean. Peripherally isolated populations are found on Santa Cruz Island off the coast of southern California, and in peninsular Florida (Pitelka 1951). The species is resident in oak woodland or pinyon-juniper woodland throughout much of its distribution, but ranges into other habitats in marginal areas (Peterson and Vargas, in press). Based on marked differentiation in morphology and plumage color, the species is divisible into five discrete "subspecies groups": the *californica* group (Oregon, California, and Baja California); the *woodhouseii* group (western Oregon and Wyoming south through the Great Basin and along the lower slopes of the Rocky Mountains and then along the Sierra Madre Oriental and Sierre Madre Occidental to central Mexico); the *sumichrasti* group (southern Mexico); the Florida populations; and the Santa Cruz Island population (Pitelka 1951). Each group is strikingly differentiated from all others in a number of plumage and morphological characters (Pitelka 1951).

I have conducted genetic studies of the species using protein electrophoresis, documenting marked genetic differentiation among populations (Peterson 1990b). Within subspecies groups, populations are usually genetically similar, differing only in allozyme frequencies. Differences among subspecies groups, however, are stronger, often involving fixed allelic differences among populations. Hence, gene flow appears to be relatively strong on a local scale, but reduced on a regional scale (Peterson 1990b).

The purpose of this study is to estimate rates of genetic exchange between the coastal (*californica*) and interior (*woodhouseii*) groups of Scrub Jays directly from an independent source of data. Using the marked differentiation in plumage characters between the two forms, I am able to employ a somewhat novel approach to estimating rates of gene flow that focuses on long-distance gene flow. These estimates are then compared to those resulting from the genetic studies.

STUDY AREA AND METHODS

The *californica* and *woodhouseii* groups of Scrub Jays are separated from each other by a series of geographic barriers, chiefly deserts (Fig. 1). In the study area, *californica* populations are restricted to oak woodland and scattered patches of pinyon-juniper woodland, and *woodhouseii* populations range in the pinyon-juniper, pinyon-juniper-oak and oak woodlands of Nevada and Arizona. In the northern Great Basin, *californica* populations are distributed in pine-oak and riparian woodlands south to the vicinity of Lake Tahoe; *woodhouseii* populations are 100–150 km distant across the deserts of northwestern Nevada in scattered desert mountain ranges. Farther south, the two forms approach one another closely (to about 20 km) in the Owens Valley of eastern California: *californica* populations are in the pinyon and riparian woodlands on the west wall, whereas *woodhouseii* populations are in the pinyon-juniper woodlands high in the White and Inyo mountains that form the east wall of the valley. Finally, in southern California, the two forms are separated by wide expanses (100 km or more) of open desert (the Mojave and Colorado River deserts).

The two Scrub Jay forms differ strikingly in a number of features. Overall, *californica* jays are deep blue (approaching purplish in southern California) dorsally and clean white ventrally, whereas *woodhouseii* jays are light gray-blue

dorsally and smoky gray ventrally. In addition, *californica* jays have a pronounced blue collar (lacking in *woodhouseii* jays), a brown back (blue-gray in *woodhouseii* jays), whitish or grayish under-tail coverts (blue in *woodhouseii* jays), and a hooked bill (generally straighter in *woodhouseii* jays; Pitelka 1951).

I evaluated a total of 2,647 specimens from the study area. I either visited or borrowed specimens from 22 museum collections: Academy of Natural Sciences of Philadelphia (ANSP), A. R. Phillips' private collection in Monterrey, Mexico (ARP), American Museum of Natural History, California State University at Long Beach (CSULB), Carnegie Museum of Natural History, Chicago Academy of Sciences (ChicASci), Delaware Museum of Natural History, Field Museum of Natural History (FMNH), Harvard University Museum of Comparative Zoology, Instituto de Biología of the Universidad Nacional Autónoma de México, Los Angeles County Museum of Natural History (LACM), Louisiana State University Museum of Natural Science, Museo de Zoología of the Facultad de Ciencias of the Universidad Nacional Autónoma de México, Museum of Vertebrate Zoology of the University of California at Berkeley (MVZ), Nevada State Museum (NSM), San Bernardino County Museum of Natural History (SBCM), University of California at Los Angeles (UCLA), University of Michigan Museum of Zoology (UMMZ), University of Nevada at Reno, U.S. National Museum of Natural History (USNM), Western Foundation of Vertebrate Zoology, and the Yale Peabody Museum. A few additional records were included based on information provided by the San Diego County Museum of Natural History (SD).

Each specimen was identified to subspecies or at least to subspecies group, and label data recorded. Collection localities were later grouped for analysis as follows. The study area was divided into six two-degree latitudinal bands on either side of the desert barrier (WW1-6, EE1-6; Fig. 1): these served as the major "source areas" for analysis. Additionally, specimens from 13 areas immediately adjacent to the desert barrier (WZ1-9, EZ1-4), and four desert zones (D1-4) were included in the analysis (Fig. 1).

Rates of gene flow were calculated as the proportion of the total sample from a region that showed influence from the other subspecies group. To the extent that strange individuals were se-
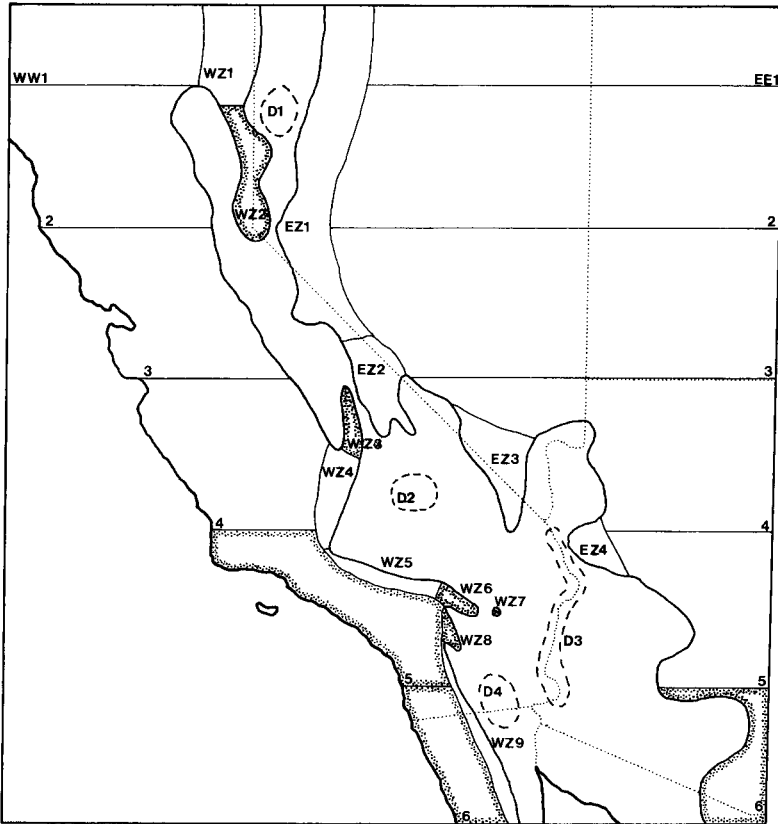
FIGURE 1. Map of the study area showing the ranges of the *californica* and *woodhouseii* groups of Scrub Jays, the sampling regions employed in this study, and the occurrence of immigrant individuals in each region (stippled areas).

lectively collected, these estimates may represent an upper bound on actual rates. These individuals were further divided into "pure" (i.e., putative first-generation immigrants) and "mixed" (apparent products of hybridization between the two forms) individuals, based on the plumage and morphological characters described above (Pitelka 1951).

RESULTS

Specimens representing immigrants or intergrades are summarized in the Appendix. Eight individuals apparently represent actual first-generation immigrants; of these, seven are *woodhouseii* jays (subspecies *nevadae*) collected in California, and one is a *californica* jay (subspecies *obscura*) collected in southern Arizona. Nineteen additional specimens appear to be intergrades because their plumages are either in-

termediate or a mixture of traits of the two forms. All intergrades were found west of the desert barrier among *californica* populations.

Rates of immigration (as indexed by proportional representation of immigrants or intergrades) differ strongly between the two subspecies groups (Table 1). Several *californica* samples include a large number of apparent immigrants: proportional representation is as high as 4.7% in populations east of the northern Sierra Nevada, 7.5% in the Little San Bernardino Mountains of southern California, and 16.0% along the west wall of the Owens Valley. All three specimens available from Eagle Mountain in southern California are apparent intergrades (Peterson 1990a). In contrast, only one apparent immigrant was found among all 546 *woodhouseii* specimens examined. The overall proportion of immigrants and intergrades is 1.25×10^{-2} in *californica* populations, and 1.83×10^{-3} in *woodhouseii* pop-

TABLE 1. Summary of sample sizes in each region and proportional levels of gene flow. P indicates apparently pure (first-generation) immigrants; M indicates individuals showing a mixture of traits of interior and coastal populations.

Region	Description	Total immigrants	Sample size	Proportion
WW1	Northernmost California	0	33	0.0
WW2	Northern California	0	146	0.0
WW3	Central California	0	568	0.0
WW4	Central-southern California	0	211	0.0
WW5	Los Angeles area	1 (P)	328	3.05×10^{-3}
WW6	Southernmost California and northern Baja California	1? (P)	204	4.90×10^{-3}
WZ1	Northeastern California	0	72	0.0
WZ2	East of Sierra Nevada	4 (2P, 2M)	85	4.71×10^{-2}
WZ3	Owens Valley	8 (2P, 6M)	50	0.16
WZ4	Kern County	0	48	0.0
WZ5	North Slope, San Gabriel and San Bernardino Mountains	0	71	0.0
WZ6	Little San Bernardino Mountains	8 (1P, 7M)	107	7.48×10^{-2}
WZ7	Eagle Mountain	3 (3M)	3	1.0
WZ8	Desert-edge ranges, Southern California and northernmost Baja California	1 (M)	102	9.80×10^{-3}
WZ9	Sierra de Juárez and Sierra San Pedro Martir, Baja California	0	56	0.0
EZ1	Western Nevada	0	9	0.0
EZ2	White-Inyo and Death Valley Ranges	0	104	0.0
EZ3	Southern Nevada, East Mojave	0	97	0.0
EZ4	Hualapai Mountains	0	4	0.0
EE1	Northernmost Nevada	0	2	0.0
EE2	North-central Nevada	0	51	0.0
EE3	South-central Nevada	0	23	0.0
EE4	Southern Nevada, Northern Arizona	0	43	0.0
EE5	Central Arizona	0	71	0.0
EE6	Southern Arizona	1 (P)	142	7.04×10^{-3}

ulations. The difference between the two populations is statistically significant (poisson distribution, $\mu = 6.81$, $n = 546$, $X = 1$, $P < 0.008$).

Seventeen specimens collected from the intervening deserts represent wandering individuals rather than resident populations (Pitelka 1951; Table 2). Four specimens (three *nevadae*, one representing an undetermined *californica* group population), have been collected from the desert lowlands of the Owens Valley. Single specimens (both *nevadae*) have been taken from Harper Dry Lake in San Bernardino County (E. Cardiff, pers. comm.) and the Salton Sea (P. Unitt, pers. comm.). Eleven individuals (10 *nevadae*, one *californica* not identified to subspecies) have been collected from along the Colorado River. All of these wandering individuals are subadults (second year), a trend pointed out previously by Pitelka (1945, 1951). Once again, a directional bias is evident, both in the Colorado River sample and in all 17 individuals: vagrants from the east

TABLE 2. Summary of origin of individuals collected in intermediate areas.

Locality	Western	Eastern	Significance
CA, Inyo Co., Owens Valley	1	3	—
CA, San Bernardino Co., Harper Dry Lake	0	1	—
CA/AZ, Colorado River	1	10	$P \leq 0.001$
CA, Salton Sea	0	1	—
TOTAL	2	15	$P \leq 0.001$

greatly outnumber those from the west (Table 2; sign tests, $P \leq 0.001$).

As described above, the overall proportion of individuals showing influence from populations of the "other" subspecies group is 1.25×10^{-2} in *californica* populations, and 1.83×10^{-3} in *woodhouseii* populations. For estimates of actual gene flow, these figures perhaps should be adjusted to include only actual immigrants rather than any individual showing influence of the other form. Hence, because only 7 of 2,084 individuals from *californica* populations are pure *nevadae*, a revised, minimum estimate of rate of gene flow would be 3.36×10^{-3}. The estimate for *woodhouseii* populations needs no adjustment because the one *californica* group individual found is apparently a first-generation immigrant.

DISCUSSION

POSSIBLE PROBLEMS

Four potential sources of error in interpretation of the above data must be considered. First, errors on specimen labels may have produced apparent examples of gene flow. Especially on older specimens, locality data are occasionally vague or misleading. However, in 18 of the 44 cases, I or others (F. A. Pitelka, pers. comm.) have personally verified the locality with the actual collector. For another 12 examples, evidence from field notes and other specimens collected strongly indicates that the records are indeed accurate. Hence, although label errors might account for some of the supposed examples of gene flow, at least 30 of the 44 cases are unlikely to be due to label error.

A potentially more serious problem is that the examples of gene flow, especially specimens identified as intergrades, might simply be extreme variants rather than examples of gene flow. I consider this unlikely for two reasons. First, intergrades invariably show influence of the other subspecies group in several characters; e.g., an individual that is exceptionally light gray dorsally in a *californica* population almost invariably has a straight bill, an indistinct collar, and bluish under-tail coverts. If these characters are segregating independently, such a correlation in their occurrence would not be expected. Second, intergrades are concentrated in the three areas most likely to receive genetic input from *wood-*

houseii populations; no intergrades were detected in coastal areas remote from interior populations. A similar complication is that the "immigrants" might actually be carrying a rare primitive allele that resembles the other form; I consider this unlikely for the same two reasons as for the "extreme variant" problem.

Third, true gene flow must be distinguished from the simple presence of vagrants that are unable to obtain mates and breed (i.e., reproductive isolation). It appears that immigrant Scrub Jays are able to breed, given that at least one (MVZ 84947) had a well-developed brood patch and was feeding young when collected. The presence of numerous intergrades indicates that offspring of such breeding attempts do survive to maturity and breed themselves.

Finally, it is possible that these rate estimates are inflated due to selective shooting of strange (i.e., immigrant) individuals. Based on conversations with several of the collectors and on personal experience collecting Scrub Jays, I believe this possibility to be unlikely: although the characters differentiating the two forms are obvious in the hand, they are difficult to see in the field. Hence, for instance, in the series of nearly 50 specimens collected by Pitelka and his field teams in the Owens Valley (Pitelka 1951), I doubt that immigrants or intergrades were selectively shot.

DIRECTIONAL BIAS

Gene flow documented in this study is strongly biased toward east-west, rather than west-east, movement. The bias in Scrub Jays appears to be part of a trend in many species. Miller and Stebbins (1964) and Peterson (1990a) argued for ongoing or historical gene flow from the Great Basin in two or three species resident on Eagle Mountain in southern California. Johnson and Garrett (1974) documented expansions of breeding range from the east into southern California by eight species. Additional examples of this trend can be found in Miller (1947) and recent issues of *American Birds*, but little evidence exists for gene flow or range expansion in the reverse direction. Hence, the east-west bias in gene flow may be more general than in just Scrub Jays.

In Scrub Jays, a reason for the bias seems evident. *Californica* jays live almost exclusively in oak woodlands, whereas *woodhouseii* jays live mostly in pinyon-juniper woodlands (Pitelka 1951, Peterson and Vargas, in press). Because

pinyon-juniper woodland seems to grade directly into desert habitats, but oak woodland tends to be more separated spatially and distinct structurally from desert, I believe that a stronger psychological barrier to entering desert habitats exists for *californica* jays. Other reasons might include differences in temporal stability of nut crops or availability of breeding space in the two habitats.

The directional bias in gene flow has implications for theoretical treatments. In discrete-subpopulation migration models, genetic interchange among subpopulations is usually summarized in a migration matrix. Migration matrices, however can take two forms: the "backward" matrix M_{ij} summarizes the proportion of individuals in population i that immigrated from population j, whereas the "forward" matrix M^*_{ij} gives the proportion of offspring in population i in one generation that will breed in population j in the next generation (Slatkin 1985a). For mathematical simplicity, theoretical treatments commonly assume symmetry of gene flow, i.e., that $M_{ij} = M^*_{ij}$ (Slatkin 1985a). This assumption is clearly not satisfied in the case of Scrub Jays, and if such directional biases are common in other natural populations, the applicability of treatments based on this assumption may need to be reevaluated.

RATES OF GENE FLOW

Calculations of rates of gene flow based on all *californica* populations suggest that 0.34–1.25% of the population represent immigrants or intergrades. Considering only the desert-edge populations, genetic interchange is strong. In the populations of the west wall of the Owens Valley, 16% of individuals show eastern influence, and 4% are apparently first-generation immigrants (Pitelka 1951). The isolated population of Eagle Mountain in southern California appears to be a mixture of the two forms, either through hybridization or due to historical intermediacy (Peterson 1990a). In *woodhouseii* populations, 0.18% of individuals are apparent immigrants. Hence, genetic exchange between the two subspecies groups occurs at appreciable frequencies.

The effects of gene flow can be best understood in conjunction with information on effective population sizes: if the product of the immigration rate m and effective population size N exceeds one, then differentiation by genetic drift

alone is unlikely (Wright 1931, Slatkin 1985a). Unfortunately, precise estimates of effective population sizes are unavailable for western North American Scrub Jays, or in fact for almost any bird species. Based on estimates of dispersal distances and population densities for Florida Scrub Jays, Woolfenden and Fitzpatrick (1984) estimated an effective population size of 298 individuals; incorporation of the effects of variance in reproductive success reduces the estimate to 20–40 individuals (J. W. Fitzpatrick, pers. comm.). These estimates are of little use in the present study, however, because the Florida population has a social system characterized by dispersal profiles very different from those of western populations (Woolfenden and Fitzpatrick 1984). Because of long dispersal distances in western Scrub Jay populations (D. B. Burt, pers. comm.; W. Carmen, pers. comm.; C. T. Collins, pers. comm.; M. J. Elpers, pers. comm.), it is almost certain that effective population sizes in western Scrub Jay populations are much higher than those of Florida Scrub Jays.

However, because of the disparity of immigration rates for *californica* and *woodhouseii* populations, an interesting situation exists (Fig. 2). If effective population sizes fall in the approximate range 100–550, then *woodhouseii* populations should be able to differentiate from the ancestral state by genetic drift (based on the estimate of m for *woodhouseii* populations), but *californica* populations should not (based on minimum and maximum estimates of m for *californica* populations). In other words, if effective population sizes are similar in the two groups (an assumption that should be tested), due to the asymmetry of gene flow between the two subspecies groups, the rate of differentiation from the ancestral state should be higher in *woodhouseii* populations than in *californica* populations. This prediction, however, does not seem to be borne out in preliminary analyses of rates of molecular evolution (Peterson 1990b, in prep.).

Based on electrophoretic studies of 10 *californica*, 11 *woodhouseii*, and 2 *sumichrasti* populations of Scrub Jays (Peterson 1990b), I estimated the gene flow parameter Nm at 4.166 using the private alleles method of Slatkin (1985b). Unfortunately, because these indirect methods are unable to separate N and m, direct comparison is difficult. Nonetheless, the direct and indirect estimates are comparable if effective pop-
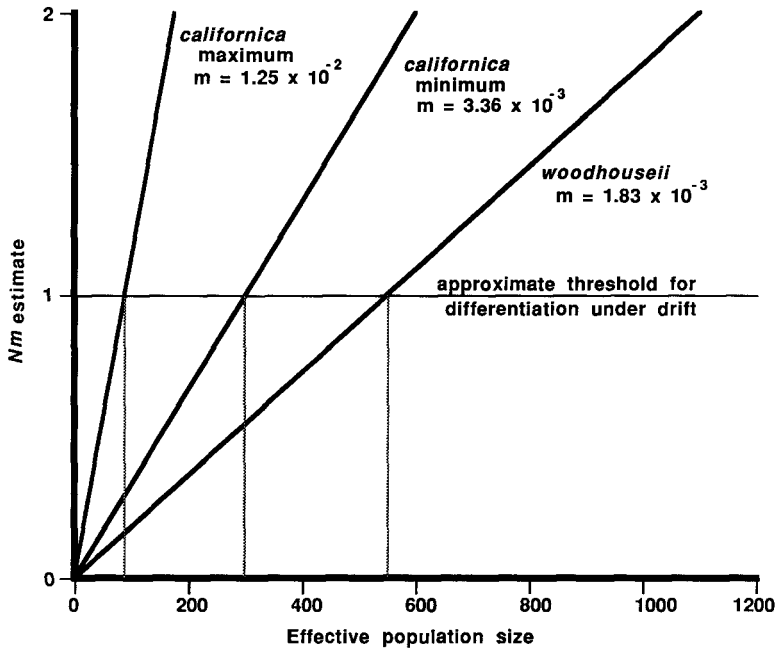
FIGURE 2. Possible combinations of effective population sizes N and immigration rates m. Approximate conditions for differentiation under genetic drift alone ($Nm < 1$) are shown, and the dotted lines indicate threshold effective population sizes for differentiation by drift alone based on the estimates of m produced in this study.

ulation sizes fall in the range 333–2,274 individuals.

CONCLUSIONS

In the present study, the rate and directionality of gene flow between two differentiated forms of Scrub Jays is documented. Immigration rates in the two forms are 0.2–1.2%; these rates are sufficient to prevent differentiation of both forms by genetic drift alone if effective population sizes exceed about 550 individuals (Wright 1931). Movement east-to-west across the Mojave Desert is two to seven times greater than west-to-east movement. This directional bias has theoretical implications because an important assumption (directional symmetry of gene flow) of most theoretical treatments of the subject is violated. Finally, if effective population sizes are comparable, the biased gene flow should lead to an overall greater rate of differentiation in *wood-houseii* populations, but this prediction is not supported in preliminary tests. This study serves to emphasize the importance of continued collecting even in well-known areas such as the United States, especially of vagrants and where long, single-locality series can be prepared.

LITERATURE CITED

EHRLICH, P. R., AND P. H. RAVEN. 1969. Differentiation of populations. Science 165:1228–1232.

ENDLER, J. A. 1977. Geographic variation, speciation, and clines. Princeton Univ. Press, Princeton, NJ.

ENDLER, J. A. 1973. Gene flow and population differentiation. Science 179:243–250.

JOHNSON, N. K., AND K. L. GARRETT. 1974. Interior bird species expand breeding ranges into southern California. Western Birds 5:45–56.

MAYR, E. 1963. Animal species and evolution. Belknap Press, Cambridge, MA.

MILLER, A. H. 1947. Arizona race of Acorn Woodpecker vagrant in California. Condor 49:171.

MILLER, A. H., AND R. C. STEBBINS. 1964. The lives of desert animals in Joshua Tree National Monument. Univ. Calif. Press, Berkeley, CA.

PETERSON, A. T. 1990a. Birds of Eagle Mountain, Joshua Tree National Monument, California. Western Birds.

PETERSON, A. T. 1990b. Evolutionary relationships of the Aphelocoma jays. Ph.D.diss., Univ. of Chicago, Chicago.

PETERSON, A. T., AND N. VARGAS B. In press. Ecological diversity in Scrub Jays (Aphelocoma coe-

rulescens). In T. P. Ramamoorthy, J. Fa, and R. Bye, [eds.], The biological diversity of Mexico Oxford Univ. Press, Oxford, England.

PITELKA, F. A. 1945. Pterylography, molt, and age determination of American jays of the genus Aphelocoma. Condor 47:229–260.

PITELKA, F. A. 1951. Speciation and ecologic distribution in American jays of the genus Aphelocoma. Univ. Calif. Publ. Zool. 50:195–464.

SLATKIN, M. 1985a. Gene flow in natural populations. Ann. Rev. Ecol. Syst. 16:393–430.

SLATKIN, M. 1985b. Rare alleles as indicators of gene flow. Evolution 39:53–65.

SLATKIN, M. 1987. Gene flow and the geographic structure of natural populations. Science 236:787–792.

WRIGHT, S. 1931. Evolution in Mendelian populations. Genetics 16:97–159.

APPENDIX.   Summary of examples of gene flow between coastal and interior Scrub Jay populations.

Locality	Museum no./ref.	Description
East-west movement		
NV, Granite Mountains	USNM 139709	pure *nevadae*
NV, Sutcliffe	LACM 22431	pure *nevadae*
NV, Ormsby Co., Kings Cyn.	NSM 1050	juvenile with bluish chest as in *nevadae*
NV, Reno	USNM 531739	as *nevadae* in color of chest and belly
NV, Gardnerville	MVZ 118704-6	towards *nevadae*
CA, Inyo Co., west wall,	MVZ 22504	pure *nevadae* (Pitelka 1951)
Owens Valley	MVZ 20077	pure *nevadae* (Pitelka 1951)
	MVZ 84936	intermediate (Pitelka 1951)
	MVZ 84970	intermediate (Pitelka 1951)
	MVZ 20068	intermediate (Pitelka 1951)
	MVZ 84952	intermediate (Pitelka 1951)
	MVZ 84946	intermediate (Pitelka 1951)
	MVZ 84950	intermediate (Pitelka 1951)
CA, Riverside Co., J.T.N.M., Lower Covington Flats	CSULB 3807	as *nevadae* in straight beak, blue of pileum
CA, Riverside Co.,	CSULB 3825	pure *nevadae*
J.T.N.M., Upper Covington Flats	CSULB 3852	apparent F1 hybrid
CA, Riverside Co.,	MVZ 94204	intermediate in several characters (Pitelka 1951)
J.T.N.M., Eagle Mountain	MVZ 94205	intermediate in several characters (Pitelka 1951)
tain	MVZ 93535	intermediate in several characters (Pitelka 1951)
CA, Riverside Co., Coleman Tin Mine	CSULB 623	as *nevadae* in blue of pileum
	CSULB 642	as *nevadae* in blue of pileum and gray breast
CA, Colton	ANSP 27922	pure *nevadae*
CA, San Diego or San Bernardino	ANSP 33854	pure *nevadae*, but tag possibly inaccurate
Baja Calif. Norte, Alaska	Pitelka 1951	intermediate
West-east movement		
AZ, Dos Cabezos [sic]	ChicASci 394	pure *obscura*
Intermediate areas		
CA, Inyo Co., Owens Valley	UCLA K786	*nevadae*
	UCLA K789	*nevadae*
	UMMZ 129341	*nevadae*
	USNM 139602	*californica* group
CA, San Bernardino Co., Harper Dry Lake	E. Cardiff, pers. comm.	*nevadae*
CA/AZ, Colorado River	LACM 46037	*nevadae*
	SBCoMNH 36420	*nevadae*
	USNM 393492	*nevadae*
	ARP 163	*nevadae*
	ARP 819	*nevadae*
	MVZ 146111	*nevadae*
	MVZ 146112	*nevadae*
	SDCoMNH 22173	*nevadae*
	SDCoMNH 32174	*nevadae*
	SDCoMNH 11318	*nevadae*
	USNM 2841	*californica* group
CA, Salton Sea	P. Unitt, pers. comm.	*nevadae*