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Population Structure and Relatedness among Female Northern Pintails in Three California Wintering Regions

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Abstract.—Female Northern Pintails (*Anas acuta*) were sampled in California's three main Central Valley wintering regions (Sacramento Valley, Suisun Marsh, San Joaquin Valley) during September-October before most regional movements occur and microsatellite and mitochondrial DNA were analyzed to examine population structure and relatedness. Despite reportedly high rates of early-fall pairing and regional fidelity, both sets of markers indicated that there was little overall genetic structuring by region. Pintails from Suisun Marsh did exhibit higher relatedness among individuals and capture groups than in the Sacramento or San Joaquin Valleys, likely reflecting a sample comprised of a greater proportion of local breeders. The lack of genetic structuring among regions indicates that a high degree of movement and interchange occurs among pintails wintering in the Central Valley. Thus, although maintaining the existing distribution of pintails among Central Valley regions is important for other reasons, it does not appear to be critical to retain current patterns of population genetic variation. Because of potential lack of independence among highly related study individuals, researchers should consider regional differences in relatedness when designing sampling schemes and interpreting research findings. *Received 25 February 2009, accepted 1 April 2009.*

Key words.—*Anas acuta*, California, Central Valley, DNA, genetics, Northern Pintail, relatedness.

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Effective management and research of Northern Pintails (*Anas acuta*) requires an understanding of their population structure. Like many waterfowl species, pintails form pair bonds during winter (Bellrose 1980; Austin and Miller 1995) and patterns of gene flow and genetic structure may be defined more during winter than during the breeding season (Robertson and Cooke 1999). About half of the pintails in North America winter in the Central Valley of California (Bellrose 1980; Central Valley Joint Venture 2006). Pintails are wide-ranging (Bellrose 1980) and previous analyses have found little evidence of genetic structure among continental pintail populations (Cronin *et al.* 1996). During the non-breeding season, birds from different breeding areas may congregate and mix. Accordingly, we might anticipate that there would be little evidence of genetic structure on the wintering grounds. However, several aspects of pintail ecology in the Central Valley could promote some degree of population structuring. The Central Valley is comprised of three main regions: 1) Sacramento Valley (northern part of the Central Valley), 2) Suisun Marsh and adjacent Sacramento-San Joaquin River Delta, and 3) San Joaquin Valley (southern part of the Central Valley) (Fig. 1). Banding data indicate that female pintails exhibit high fidelity (Rienecker 1987; Hestbeck 1993) to these Central Valley regions, returning each winter as early as the first week of August (Miller 1985). Radio-tracking of female pintails captured during late August through early October in the three regions shows that although there was a high degree of inter-regional

Figure 1. The Central Valley of California including the three main Northern Pintail (*Anas acuta*) wintering regions (Sacramento Valley, Suisun Marsh-Sacramento-San Joaquin River Delta, and San Joaquin Valley). Female Pintails were sampled at Sacramento National Wildlife Refuge, Suisun Marsh, Grassland Ecological Area, and Mendota Wildlife Area.

movement, mostly from Suisun Marsh and San Joaquin Valley into Sacramento Valley, most regional interchange did not occur until November-December (Casazza 1995; Miller *et al.* 1995; Fleskes *et al.* 2002, 2005). Many Central Valley pintails form pair bonds early in winter, with 55% already paired by mid-November (Miller 1985). Thus, many pintails in the Central Valley likely pair and breed with individuals in the region where they started winter. The impact on pintail population genetic structure of the relatively high wintering region fidelity and formation of pair bonds before most regional mixing occurs is unknown.

Unlike most other North American dabbling ducks, abundance of Northern Pintails remains well below their long-term average and North American Waterfowl Management Plan goals (USFWS and Canadian Wildlife Service 1986; Zimpfer *et al.* 2008). Overall abundance of pintails in the Central Valley has declined since the 1970s (Pacific Flyway waterfowl reports and USFWS, Portland, Oregon, USA, unpublished data), tracking continental trends (Zimpfer *et al.* 2008). However, the decline in abundance has been greater in Suisun Marsh and San Joaquin Valley than in Sacramento Valley (Michny 1979; Fleskes *et al.* 2002), and by 1998-2000, only about 4% of the pintails in Central Valley during September-March were in Suisun Marsh and adjacent San Joaquin-Sacramento River Delta, 22% were in San Joaquin Valley, and 74% were in Sacramento Valley. Although, habitat changes in the Central Valley are thought to explain much of the redistribution of wintering pintails in the Central Valley (Fleskes *et al.* 2002; 2005), an understanding of the population genetic structure of pintails wintering in each Central Valley region would help to interpret population trends and guide pintail management and research (Rhodes *et al.* 1991). For example, differences in mitochondrial DNA (mtDNA) haplotype frequencies among Central Valley regions could reflect population structure among breeding areas and require different habitat management or harvest recommendations for wintering pintails. Local structuring of populations (e.g., differences in relatedness among regions) could also impact sampling design considerations and interpretation of research findings. To inform pintail research and management we used mitochondrial and microsatellite DNA to describe the population genetic structure and relatedness of pintails present during fall in the three main Central Valley wintering regions.

METHODS

Sample Collection and Analysis

We collected samples from a randomly selected subset of the female pintails that we captured during fall 1999 in each of the three main pintail wintering regions in the Central Valley. We captured 3-37 (mean = 22, SE = 7.4) female pintails at each of four rocket net shots (Schemnitz 1994) during 31 August-2 September at Sacramento National Wildlife Refuge in the Sacramento Valley, 5-41 (mean = 19, SE = 7.1) female pintails at each of five rocket net shots during 9-22 September at Grizzly Island Wildlife Area in Suisun Marsh, and 2-28 (mean =

15, SE = 5.3) female pintails at each of five rocket net shots during 5-22 September in San Joaquin Valley (one capture of 28 female pintails at Mendota Wildlife Area [MWA] and four captures of 2-24 female pintails at the Grassland Ecological Area [GEA] Fig. 1). We extracted DNA for microsatellite analyses from 70 blood samples collected from 20 Hatch-Year (HY) and two After-Hatch-Year (Carney 1992) females in the Sacramento Valley, 26 HY females in Suisun Marsh, and 22 HY females in San Joaquin Valley (twelve from MWA and ten from GEA). Template DNA was extracted from blood samples using QIAamp DNA Blood Mini Kit (QIAGEN, Incorporated, Valencia, California). We also extracted DNA for mtDNA analyses from 27 feather samples collected from nine females in Sacramento Valley, ten in Suisun Marsh, and eight in San Joaquin Valley (four from MWA and four from GEA); six individuals in this analysis were also represented by blood samples. For feather extraction, we used either PUREGENE DNA Isolation Kits (Gentra Systems, Incorporated, Minneapolis, Minnesota) or QIAGEN DNeasy Tissue Kits. We used eleven microsatellites that were developed for other waterfowl species (ANAS [Cathey *et al.* 1996]; Sfiu4, Sfiu5, and Sfiu7 [Fields and Scribner 1997]; Bcau10, Bcau11 and Hhiu5 [Buchholz *et al.* 1998]; Aph01, Aph07, and Aph09 [Maak *et al.* 2000]; Sfiu8 [Libants *et al.* unpublished sequence #AF180498]) to examine spatial genetic variation in pintails. Each microsatellite locus was amplified in 10 ul reaction volumes containing 1.5 ul template DNA, 1X PCR buffer (20mM Tris-HCl pH 8.4, 50mM KCl), 1.0-2.0mM $MgCl_2$ (ANAS, Hhiu5, Aph01, Aph07, Aph09, and Sfiu8, 1.0mM, Sfiu4, Sfiu5, Sfiu7, and Bcau11, 1.5mM, Bcau10, 2.0mM), 200 uM dNTPs, 10 ug/mL Bovine Serum Albumen, 0.5 units Taq DNA polymerase (Invitrogen, Life Technologies, Carlsbad, California), and 0.4 uM unlabeled and 5' fluorescein-labeled primers. Thermocycler conditions for PCR consisted of one cycle of 94°C denaturation for 2 min and 25-35 cycles of locus-specific annealing temperatures (Sfiu5 and Aph07, 50°C, Sfiu7, 52°C, Aph01, and Aph09, 54°C, ANAS, Sfiu8 Bcau10, Bcau11 and Hhiu5, 55°C, Sfiu4, 58°C) for 45 s, 72°C extension for 45 s, and 94°C denaturation for 45 s, followed by one cycle of locus-specific annealing for 1 min and 72°C extension for 5-10 min. Amplification products were mixed 1:1.5 with 98% formamide loading dye, denatured for 3-5 min at 95°C and cooled on ice before separating on 5.5% denaturing polyacrylamide gel at 35 W for about 1 h. Unlabeled products were detected using the agarose and Vistra Green (Amersham Biosciences, Incorporated, Piscataway, New Jersey) overlay procedure of Rodzen *et al.* (1998). Fluorescein-labeled and Vistra Green stained products were scanned with a Molecular DynamicsTM FluorimagerTM 595 (Molecular Dynamics, Sunnyvale, California) and assigned scores using a fluorescein- labeled 10-bp ladder (The Gel Company, San Francisco, California).

An approximately 560-bp fragment of the 5' end of the mtDNA control region was amplified using the template DNA extracted from feathers. Control region primers included Sorenson and Fleischer's (1996) L78 and Sorenson *et al.*'s (1999) H774. PCR was carried out in 50 ul reactions containing 10 ul of template DNA, 1X GeneAmp PCR Gold Buffer (Applied Biosystems, Foster City, California, 15 mM Tris-HCl pH 8.0, 50 mM KCl), 1.25mM $MgCl_2$, 200 uM dNTP's, 0.5 M of each primer and 1.0 units AmpliTaq Gold (Applied Biosystems, Foster City, California). Thermocycler conditions for PCR consisted of one cycle of 95°C denaturation for 10 min and 35 cycles of 58°C annealing temperature for 1 min, 72°C extension for 1.5 min, and 94°C denaturation for 45 s, followed by one cycle of 58°C annealing for 1 min and 72°C extension for 10 min. Entire PCR products were electrophoresed in a 1.2% agarose gel at 100 volts for about 1 h, excised and gel-purified using a QIAquick Gel Extraction Kit (QIAGEN, Incorporated, Valencia, California). Products were cycle-sequenced using BigDye version 3 at the Department of Biological Sciences Automated Sequencing Laboratory, University of California, Davis, California. Samples were sequenced in both directions and reconciled and aligned using ClustalX (Thompson *et al.* 1997). Sequences have been submitted to GenBank (Accession Numbers: FJ713459-FJ713474).

Data Analysis

We used POPGENE version 1.21 (Yeh *et al.* 1997) to calculate the average numbers of alleles per locus, expected (H_e unbiased for sample size) and observed heterozygosities (H_o) at each locus for pintails grouped by Central Valley region, and tested for departures from Hardy-Weinburg equilibrium at each locus in a global test (all regions pooled). We pooled pintails captured at MWA and GEA into the same Central Valley regional group (i.e. San Joaquin Valley) because these sites were only 40 km apart (vs. approx. 150 km between Suisun Marsh and Sacramento Valley, 150 km between GEA and Suisun Marsh, and 290 km between Sacramento Valley and GEA sites, Fig. 1) and radio-tracking indicated most pintails captured in MWA moved to GEA during October (Fleskes *et al.* 2002). We used GENEPOP (version 3.3, updated [2001] version of Raymond and Rousset 1995) to test for linkage disequilibrium by regional group (Markov Chain method and Bonferroni correction [Rice 1989]) and for each locus pair across groups (Fisher's Exact Test), to calculate allele frequencies for each group at each locus and test allele frequency differences among regional group pairs (Fisher's exact test), and to calculate the number of migrants between regional groups per generation using the private allele method of Barton and Slatkin (1986). Genotypic differentiation was tested using a log-likelihood (G) based exact test; an unbiased estimate of the P-value was determined using the Markov chain method (Goudet *et al.* 1996). We estimated pair-wise differentiation between regional groups, as indicated by F_{ST}, in ARLEQUIN version 3.0 (Schneider *et al.* 2000). Significance of F_{ST} values was determined following a sequential Bonferroni correction for multiple tests. We used hierarchical analysis of molecular variance (AMOVA) in the program ARLEQUIN version 2.0 (Schneider *et al.* 2000) to further evaluate differentiation among regional groups for both microsatellite loci and mtDNA haplotypes, and to calculate pair-wise group comparisons of Φ_{ST} for mtDNA. We used the program TCS version 1.21 (Clement *et al.* 2000) to compute an unrooted haplotype network for mtDNA haplotypes based on the matrix of pair-wise differences calculated between haplotypes (Templeton *et al.* 1992).

We calculated an estimate of relatedness among females using the method of Queller and Goodnight (1989), implemented in the program Kinship version 1.3.1 (Goodnight 2000; Goodnight and Queller 1999). Relatedness (R) was calculated among females in each regional group and among females in each rocket-net

capture group within region. Because of a lack of independence in relatedness values among dyads, we used resampling techniques to test for significant differences in relatedness among regions and among capture groups within regions. We calculated the sum of absolute differences

(SB statistic: group mean $\bar{x}$ - grand mean $\bar{x}$, $\Sigma\left|(x_i + \bar{x})\right|$; Simon 1998; Blank *et al.* 1999)

as a measure of differences among the groups. To determine the significance level of this test, we randomly reshuffled the matrix of relatedness coefficients (keeping sample sizes the same for each group) and recalculated the SB statistic; we repeated this 10,000 times.

RESULTS

Data Quality

Analysis of data pooled across all rocket net capture groups and regions indicated that all loci were in Hardy-Weinberg equilibrium (Table 1), revealing no global problems with null alleles or allelic drop-out. When analyses were conducted for each region, all but two of the 33 loci were in Hardy-Weinberg equilibrium ($P > 0.05$ after Bonferroni correction). The two loci not in Hardy-Weinberg equilibrium (Sfiu8 and ANAS) were both from Suisun Marsh and deviations were due to a deficiency of heterozygotes. There was no evidence of linkage disequilibrium, either by Central Valley region (Markov Chain method, $P \geq 0.06$ before Bonferroni correction) or for each locus pair across Central Valley regions (Fisher's Method, $P \geq 0.16$). Thus, each locus can be treated as an independent marker.

Microsatellite Variation among Central Valley Regions

Analyses of microsatellites indicated no strong pattern of female pintail genetic differentiation among Central Valley regions, although there was weak evidence of regional differences at two loci. Neither allelic nor genotypic frequency differences for each locus were significant at any of the eleven loci among the three Central Valley regions, although differentiation at two (Sfiu7 and Sfiu5) were greater than at the other loci (Table 1). Estimates of F_{ST} were also higher at Sfiu7 and Sfiu5 than other loci. However, overall estimates of F_{ST} (Table 1) and pair-wise comparisons among Central Valley regions based upon microsatellite DNA (Table 2) indicate a high degree of regional interchange.

Table 1. Number of alleles, observed and expected heterozygosities, F_{ST}, and tests of allelic and genotypic differentiation (Raymond and Rousett 1995) among female Northern Pintails (*Anas actua*) in three California regions (Sacramento Valley, San Joaquin Valley and Suisun Marsh) for eleven microsatellite loci.

		Heterozygosity[1]			Differentiation P-value[2]	
Locus	Number of alleles	Observed	Expected	F_{ST}	Allelic	Genotypic
Sfiu7	3	0.286	0.277	0.046	0.025	0.015
Bcau10	5	0.343	0.315	-0.006	0.744	0.755
Hhiu5	5	0.457	0.484	-0.019	0.953	0.924
Bcau11	6	0.443	0.521	-0.020	0.535	0.618
Sfiu5	10	0.686	0.758	0.017	0.015	0.027
Aph09	9	0.686	0.720	-0.006	0.652	0.757
Sfiu4	11	0.900	0.852	0.006	0.319	0.404
Aph01	15	0.814	0.871	0.002	0.704	0.891
Sfiu8	24	0.771	0.947	-0.009	0.721	0.901
Aph07	28	0.929	0.957	0.0001	0.350	0.378
ANAS	36	0.914	0.962	-0.002	0.433	0.548
Mean ± SD	13.8 ± 10.9	0.657 ± 0.237	0.697 ± 0.257			
All				-0.0005	0.254[3]	0.389[3]

[1]Hardy-Weinberg equilibrium test not significant for any locus (P ≥ 0.28 vs. Bonferroni corrected significant P-value of 0.005).

[2]None significant at the Bonferroni corrected P-value of 0.005.

[3]P-value for Chi-square test (22 df) for overall allelic ($\chi^2 = 25.96$) or genotypic ($\chi^2 = 23.23$) differentiation.

Table 2. Pair-wise regional differences among female Northern Pintail (*Anas acuta*) for eleven microsatellite DNA loci (F_{ST} statistics above diagonal) and a 560-bp region of the mtDNA control region (Φ_{ST} statistics below diagonal). *P* values were generated by permutation tests (Schneider *et al.* 2000).

	Sacramento Valley	Suisun Marsh	San Joaquin Valley
Sacramento Valley	—	-0.010 $P = 0.77$	0.003 $P = 0.25$
Suisun Marsh	0.081 $P = 0.11$	—	-0.003 $P = 0.49$
San Joaquin Valley	-0.028 $P = 0.56$	-0.004 $P = 0.42$	—

AMOVA of the eleven microsatellite loci showed that >99% of the overall variance in genetic structure was within regions and <1% was among Central Valley regions, indicating little evidence of differentiation among Central Valley regions (Table 3a). Locus by locus AMOVA revealed that regional differences were most pronounced for Sfiu7 ($P = 0.021$) and Sfiu5 ($P = 0.07$). The estimated number of migrants between regional groups per generation, relative to our sample over all loci, ranged between 6.2 and 10.3, indicating high levels of gene flow.

Mitochondrial DNA Variation among Central Valley Regions

Analysis of mtDNA also suggested little evidence of genetic differentiation among Central Valley regions; Φ_{ST} values for all regional pairs were small and not significant (Table 2). There was considerable variation in mtDNA among Northern Pintails wintering in the Central Valley; 18 polymorphic sites were identified in the 560-bp region of the mtDNA control region resulting in 16 haplotypes among the 27 birds sampled (Table 4). However, AMOVA revealed that almost all the variation was within, rather than among, regional groups (Table 3b). Only three of the 16 haplotypes were represented by multiple individuals, with the most common haplotype (A) present in all three Central Valley regions, the second most common (I) in both Sacramento Valley and San Joaquin Valley, and the third (H) represented by two San Joaquin Valley pintails. Haplotypes represented by only a single individual were present in each region (three in Sacramento Valley, six in San Joaquin Valley and Suisun Marsh). An unrooted haplotype network for the 16 haplotypes suggests two main groups, one including the most common

Table 3. Molecular analysis of variance (AMOVA) to test for differentiation among female Northern Pintails (*Anas acuta*) in three Central Valley regions using (A) eleven microsatellite loci and (B) 18 variable sites in a 560-bp region of the mtDNA control region.

Source of Variation	df	Sum of squares	Variance components	Percentage of Variation
(A) Microsatellites				
Among Central Valley Regions	2	341.27	-0.76	-0.37
Within Central Valley Regions	137	28218.61	205.98	100.37
Total	139	28559.88	205.22	

Source of Variation	df	Sum of squares	Variance components	Percentage of Variation
B) mtDNA				
Among Central Valley Regions	2	3.81	0.03	1.92
Within Central Valley Regions	24	38.93	1.62	98.08
Total	26	42.74	1.65	

Table 4. Haplotypes for a 560-bp region of the mtDNA control region of female Northern Pintails (*Anas acuta*) in California.

Haplotype	23	30	81	82	97	100	123	132	133	137	146	156	163	192	202	219	245	296
A	T	T	A	A	C	C	C	T	C	C	C	C	A	A	C	C	T	C
B	•	C	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
C	•	•	•	•	T	•	•	•	•	•	•	•	•	•	•	•	•	•
D	•	•	G	G	•	•	•	•	•	•	•	•	•	•	•	•	•	•
E	•	•	•	•	•	•	•	•	•	•	•	•	•	•	T	•	•	•
F	•	C	•	•	•	•	•	•	•	•	•	•	•	•	T	•	•	•
G	•	C	•	•	•	•	•	•	•	•	•	T	•	•	T	•	•	•
H	•	•	•	•	•	•	•	C	•	•	•	•	•	•	•	•	•	•
I	C	•	•	•	T	•	•	C	•	•	•	•	•	•	•	•	C	•
J	C	•	•	•	•	T	•	•	•	•	•	•	•	•	•	•	C	•
K	C	•	•	•	•	T	•	•	•	•	•	•	G	•	•	•	C	•
L	C	•	•	•	•	•	•	•	•	•	•	•	G	•	•	•	C	•
M	C	•	•	•	•	•	•	•	•	•	•	•	•	G	•	•	C	•
N	C	•	•	•	•	•	•	•	T	•	T	•	•	•	•	T	C	•
O	C	•	•	•	•	•	T	•	•	•	•	•	•	•	•	•	C	T
P	C	•	•	•	•	•	•	•	•	T	•	T	•	•	•	•	C	•

(A) haplotype, with the next most common haplotype (I) an intermediate (Fig. 2). Pintails from all three Central Valley regions were represented by haplotypes distributed throughout the tree.

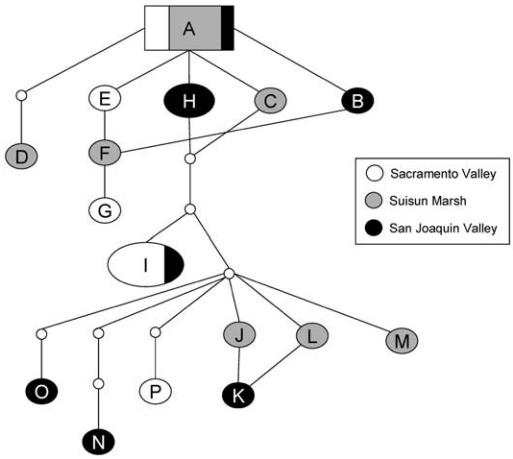

Figure 2. An unrooted network (Templeton *et al.*1992, Clement *et al.* 2000) connecting 16 haplotypes (A-P) of a 560-bp region of the mtDNA control region of 27 female Northern Pintails (*Anas acuta*) sampled during August-September 1999 in the three main wintering regions (Sacramento Valley, San Joaquin Valley, Suisun Marsh) of the Central Valley of California. Letters are unique haplotypes and the size of each circle is roughly proportional to the number of individuals with that haplotype. Only haplotypes A (n = 7 individuals), I (n = 5), and H (n = 2) were represented by more than one individual. The haplotype with the highest outgroup probability is displayed as a square, while other haplotypes are displayed as ovals. The small open circles indicate possible intermediate haplotypes that were not sampled.

Relatedness within Regions

Levels of relatedness (Queller and Goodnight 1989) were low for pintails within most Central Valley wintering regions (average R = 0.003). However, relatedness was significantly higher in Suisun Marsh than in other regions (Suisun Marsh: R = 0.031, Sacramento Valley: R = -0.025; San Joaquin Valley: R = - 0.011; SB statistic 0.0689, $P < 0.0001$; Fig. 3). Analysis of individuals by capture group (i.e. ignoring region) showed that relatedness did not differ among capture group overall (SB statistic 0.0045, $P = 0.72$). However, within region, individuals in the same capture group in Suisun Marsh were more closely related than to individuals in different Suisun Marsh capture groups (R = 0.05 vs. 0.025; SB statistic = 0.027, $P = 0.048$; Fig. 3).

DISCUSSION

Both nuclear and mitochondrial DNA markers indicated that there was little overall genetic structuring among Northern Pintails wintering in the three Central Valley regions that we examined. The fact that there is little evidence of Hardy-Weinburg disequilibrium at any of the markers examined, or any other

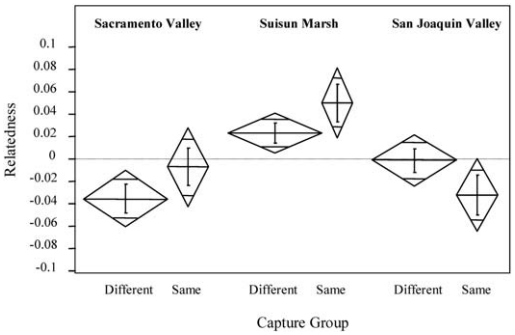

Figure 3. Relatedness (Queller and Goodnight 1989) of female Northern Pintails (*Anas acuta*) in the same or different capture groups in three main wintering regions of the Central Valley of California, August-September 1999. The horizontal center line is the population mean, the center vertical bar is the mean SE bar (1 SE above and below), the diamond vertical points are 95% confidence intervals, and the diamond width represents relative sample size.

evidence of regional genetic structuring in Central Valley pintails, despite a reported high rate of pairing before most regional mixing occurs, indicates a high degree of genetic interchange later in winter and spring and broad panmixis. Our results complement those of Cronin *et al.* (1996) who found little evidence of mtDNA differentiation among Pintails throughout North America. Given the wide ranging nature of Pintails and band-recovery data indicating extensive mixing of individuals from a variety of nesting areas on some wintering grounds (Lensink 1964), the lack of strong population genetic structure within a single wintering area is not surprising. However, our results for pintails are in contrast to data from Mallards (*Anas platyrhynchos*) and American Wigeon (*Anas americana*) wintering in Texas which indicate genetic differentiation among breeding populations (Rhodes *et al.* 1993, 1995). Likewise, Peters *et al.* (2005) found strong differentiation in mtDNA among eastern and western populations of Wood Ducks (*Aix sponsa*). In contrast, Peters and Omland (2007) found little genetic structure for Gadwall (*Anas strepera*) in North America except for differentiation of Alaska and Washington birds from other populations. Pearce *et al.* (2008) also found little evidence of genetic structure in either nuclear or mitochondrial DNA among populations of Hooded Mergansers (*Lophodytes cucullatus*) in North America, although this species was shown to have high breeding site fidelity. Pearce *et al.* (2008) argued that an accurate assessment of population delineation requires comparisons among species using multiple data types, such as mark-recapture and genetic information, to infer patterns across a range of geographic and temporal scales. We agree, and our data on pintails, coupled with previous band-recovery and radio-telemetry studies in the Central Valley, directly respond to that recommendation. Our results further reinforce Pearce *et al.*'s (2008) findings in showing that high fidelity to an area (in our case wintering regions where pair bonding occurs) does not necessarily promote population genetic structure. Clearly, patterns of gene flow vary among species of waterfowl in rather complex ways, making this an intriguing group for further study.

The higher relatedness we observed among Suisun Marsh pintails likely reflects a Suisun Marsh sample comprised of a greater proportion of local breeders rather than nonrandom mixing of individuals among regions. Pintails are more common nesters in Suisun Marsh than in the other Central Valley regions (G. Yarris, California Waterfowl Association, Sacramento, unpublished data) and the abundance of pintails in Suisun Marsh during the time we trapped was low compared to Sacramento Valley and San Joaquin Valley (e.g., on 1 October, 4% of Central Valley Pintails in Suisun Marsh, 42% in Sacramento Valley, and 54% in San Joaquin Valley during 1998-2000, Fleskes *et al.* 2005). Thus, local nesters likely comprised a much greater proportion of our sample in Suisun Marsh than in the other two regions. Casazza (1995) theorized that one reason hatch-year female pintails captured in the Suisun Marsh were especially heavy in 1991 was because many were local birds that had not suffered the weight loss caused by long migration.

Management Implications

The lack of genetic structuring among regions indicates that changes in pintail dis-

tributions among Central Valley regions (Fleskes *et al.* 2005) and differences in pintail survival among Central Valley regions (Fleskes *et al.* 2007) have little impact on the population genetic structure of pintails during winter in California. Accordingly, while restoring and maintaining historic distribution of pintails among Central Valley regions is important to ensure widespread support for habitat conservation, minimize the risk of catastrophic disease loss (Central Valley Joint Venture 2006), and retain regional opportunities for hunting and bird watching, it is not critical to maintain current patterns of population genetic structure (Rhodes *et al.* 1991). However, analyses of relatedness within populations revealed non-random patterns of relatedness that would otherwise have been overlooked. The result suggests that researchers should consider the potential lack of complete independence among study individuals when designing sampling schemes and interpreting results of studies of life-cycle parameters such as productivity and survival.

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