Conserv Genet (2013) 14:439–449
DOI 10.1007/s10592-012-0388-0

RESEARCH ARTICLE

Fine-scale social and spatial genetic structure in Sitka black-tailed deer

Kevin E. Colson · Todd J. Brinkman · David K. Person · Kris J. Hundertmark

Received: 30 January 2012 / Accepted: 13 July 2012 / Published online: 4 August 2012

Abstract The spatial extent of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) populations below the regional scale is relatively unknown, as is dispersal between populations. Here, we use noninvasive samples to genotype 221 Sitka black-tailed deer in three watersheds on Prince of Wales Island, Alaska, separated by a maximum of 44 km, using traditional and spatial genetic approaches. We find that despite geographic proximity, multiple lines of evidence suggest fine-scale genetic structure among the three study sites. The 2 most geographically distant watersheds differed significantly in genetic composition, suggesting an isolation-by-distance pattern. Within study sites, deer exhibited spatial genetic structure within a radius of 1,000 m. Based on a reduced sample of known-sex individuals, females exhibited positive spatial genetic structure within a radius of 500 m but males showed no structure. Moreover, females were more likely to be related to their 5 nearest female neighbors, regardless of distance, than were males. Evidence indicates dispersal by both sexes although it may be more common, or dispersal distances are greater, in males. Nonetheless, analysis of assignment indices and comparison of sex-specific correlograms found no evidence of sex-biased dispersal between watersheds. Patterns of spatial relatedness and connectivity suggest limited dispersal among Sitka black-tailed deer, creating genetic structure on a fine spatial scale, perhaps as small as the watershed.

Keywords Alaska · Gene flow · *Odocoileus hemionus sitkensis* · Population structure · Spatial autocorrelation

K. E. Colson (✉) · T. J. Brinkman · K. J. Hundertmark
Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775, USA
e-mail: kcolson@alaska.edu

K. J. Hundertmark
e-mail: khundert@alaska.edu

T. J. Brinkman
Scenarios Network for Alaska and Arctic Planning, University of Alaska Fairbanks, Fairbanks, AK 99709, USA

D. K. Person
Alaska Department of Fish and Game, Ketchikan, AK 99901, USA

Introduction

Sitka black-tailed deer (SBTD), *Odocoileus hemionus sitkensis,* are endemic to, and widely distributed along, the archipelago and coastal mainland of southeastern Alaska and northern British Columbia. Populations have also been introduced to Prince William Sound and the Kodiak Archipelago of southcentral Alaska. SBTD are considered an important species ecologically and economically, as well as being the most important subsistence resource in southeastern Alaska (Hanley 1993; Brinkman et al. 2007). Whereas previous studies have assessed movement, habitat use, nutrition, survival, and abundance of SBTD (Schoen and Kirchhoff 1985, 1990; Yeo and Peek 1992; Chang et al. 1995; Parker et al. 1999; Farmer et al. 2006, Brinkman et al. 2011), there is little information on the spatial scale of populations, or connectivity among populations. Only Latch et al. (2008) has researched population structure of SBTD, and that study focused on the inter-island, regional scale.

Genetic population structure is not an intrinsic feature of a species, but an emergent phenomenon resulting from the interaction of behavior, morphology, and physiology with terrain and habitat (e.g., Anthony and Blumstein 2000;

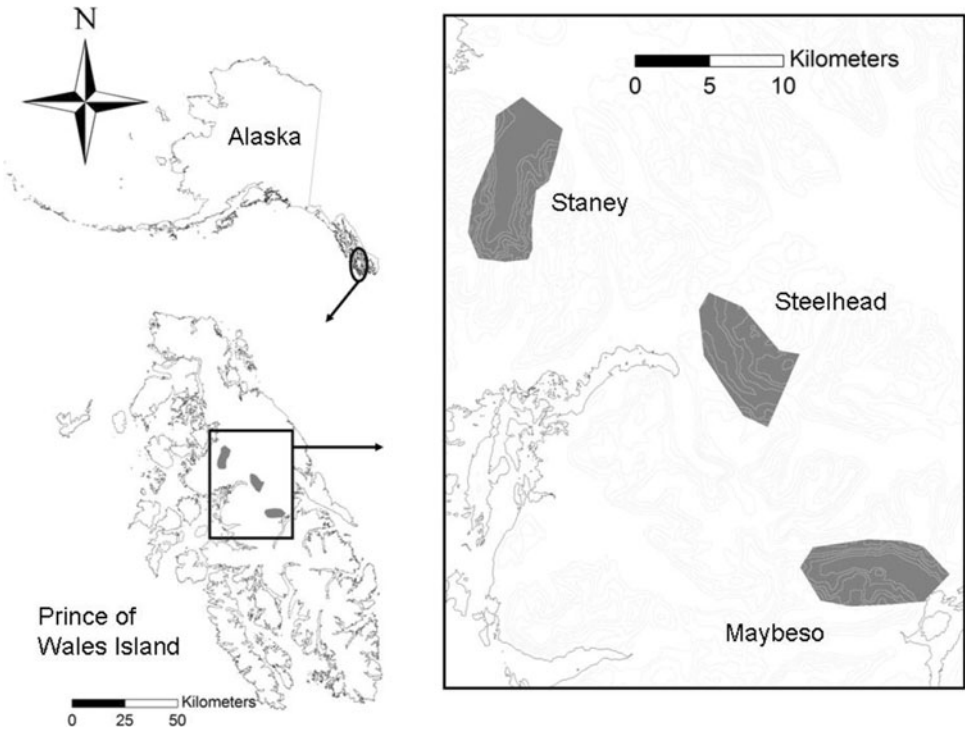

Fig. 1 Map of study sites within study area on Prince of Wales Island, Alaska, USA (after Brinkman et al. 2011)

Prugnolle et al. 2005). It can be used to understand demographic processes that might otherwise go unobserved, such as dispersal frequency (Whitlock and McCauley 1999), which is an unknown population parameter among SBTD. A broad understanding of dispersal and gene flow in a species is helpful in managing populations in a viable manner (Allendorf and Luikart 2006), which is all the more relevant for management of SBTD because it is highly contentious (Unit 2 Deer Planning Subcommittee 2005). Further, population structure affects genetic diversity, which is noted to effect components of fitness, e.g., parasite resistance (Hedrick et al. 2001), antler morphology (Hartl et al. 1991), and attractiveness (Brown 1997), as well as to important management concerns such as spread of disease (Cullingham et al. 2011; Lang and Blanchong 2012). Finally, it is important to discern the links between sociality and genetic structure in intensely managaed species (Miller et al. 2010). Insights gained from a broad understanding of connectivity and genetic population structure, especially on a fine scale (e.g., Coltman et al. 2003) would aid management of SBTD by providing a better understanding of population dynamics.

Our objective was to investigate the extent of SBTD population structure on a finer, intra-island scale that better corresponds to the spatial scale at which deer are actively managed (Kirchhoff and Pitcher 1990). We sought to characterize the level of genetic diversity in SBTD and to document a baseline of data on genetic differentiation. Using that baseline, we attempted to derive effective migration rates to better understand the spatial isolation of subpopulations, and to assess whether fine-scale patterns of relatedness follow the predictions of the rose-petal model, namely fine-scale genetic structuring caused by females tending to form home ranges overlapping with, or adjacent to, those of their mothers, as has been documented in white-tailed deer (*O. virginianus*; Porter 1991).

Study area and methods

Our research was conducted on Prince of Wales Island, Alaska, USA (Fig. 1). Prince of Wales Island is in southeastern Alaska in the Alexander Archipelago. It is the third largest island in the United States and is characterized by rugged mountains up to 1,160 m in elevation and long fjords. The majority of the island is located within the Tongass National Forest. Below 600 m elevation, habitats are primarily dominated by temperate rainforest consisting of Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*) and yellow cedar (*Chamaecyparis nootkatensis*) (Alaback 1982). The coniferous forests are a mixture of old-growth stands and clearcut-logged stands of various successional stages from 0 to 60 years old.

Our study sites were located in three watersheds inside the north central region: (1) Maybeso Creek, (2) upper Staney Creek, and (3) upper Steelhead Creek (Fig. 1), referred to hereafter as Maybeso, Staney, and Steelhead. All study sites

were accessible by roads, open to seasonal hunting, and contained similar deer densities (9–10 deer/km^2; Brinkman et al. 2011) during the time of this investigation. All watersheds were a mixture of old-growth forest, harvested timber stands, less productive hydric soils, open heath muskeg, and alpine tundra habitat (Brinkman and Hundertmark 2009). The area sampled was approximately 35.3 km^2 (Staney = 16.8 km^2, Steelhead = 9.7 km^2, Maybeso = 8.8 km^2). Maximum distance between sampling areas was approximately 44 km (Fig. 1).

Sampling design

We relied on noninvasive sampling (Kohn and Wayne 1997; Mills et al. 2000), and used DNA extracted from georeferenced deer fecal pellets to collect genetic information. Our sampling strategy and pellet collection protocol were described in detail in Brinkman et al. (2011). Briefly, during March through May 2008, we collected fecal pellets along transects in each study site. Each site experienced population closure during this sampling period, as deep snow at higher elevations forms an effective barrier against movement between watersheds (Schoen and Kirchhoff 1985; Klein and Olson 1960). During the sampling period, there was no legal harvest, no parturition, and no dispersal or migration, and deer that seasonally migrate up to alpine areas in the summer are likely to be present among resident individuals (Farmer et al. 2006). None of our sites violated our assumptions of closure (Brinkman et al. 2011).

To effectively address influence of landscape variability on distribution of deer, transects were established across varying elevations, slopes, aspects, habitat types, and at varying distances from roads and streams in each watershed. During the field season, we resampled the same transects at 10-day intervals. All pellets were removed from the transect after each collection to avoid resampling from the same pellet group during subsequent sampling occasions. Pellet samples were preserved in ethanol and shipped to the Wildlife Conservation Genetics Laboratory at the University of Alaska Fairbanks for subsequent analysis.

DNA extraction and analysis

We extracted and analyzed genomic DNA from deer fecal pellets following methods described in Brinkman et al. (2010). Briefly, we used the DNeasy Tissue Kit (Qiagen Inc. Valencia, CA), with slight modifications. Details on extraction modifications, PCR reaction volumes, PCR profiles, and error checking protocol are described in Brinkman et al. (2010). We used eight microsatellite loci (Table 1) in multiplex PCR reactions plus a locus to determine gender (Brinkman and Hundertmark 2009). Microsatellite alleles were separated on an ABI 3100 Genetic Analyzer (Applied Biosystems, Foster City, California) per the manufacturer's protocol. The electropherograms were scored manually using GeneMapper 3.7 software® (Applied Biosystems, Foster City, California).

To minimize potential genotyping error we followed a "multi-tube" approach, where DNA from each sample was amplified separately multiple times (Taberlet et al. 1996; Bellemain et al. 2005). After scoring genotypes, we employed Micro-Checker (van Oosterhout et al. 2004), a program that aids in detecting stutter bands, erroneous allele scores, null alleles, and allelic dropout. Samples were analyzed in Micro-Checker by study site.

Genetic diversity

We used GenAlEx v6.4 (Peakall and Smouse 2006) to identify unique individuals within each study site through multilocus matching. We required an exact genotype match at all loci to identify two samples as coming from the same individual. Each identified individual was used once, and any subsequent resamplings were excluded from analyses.

A series of tests were performed to provide baseline parameters of genetic diversity for deer populations in each

Table 1 Diversity and characteristics of markers used for this study

Locus	Alleles	A_{52}	Allelic range	H_o	H_s	HWE	Reference
SBTD06	3	2.235	176–188	0.472	0.493	0.035	Brinkman et al. (2010)
C89	2	2.000	161–169	0.199	0.184	0.993	Levine et al. (2000)
SBTD04	7	5.765	242–302	0.660	0.655	0.742	Brinkman et al. (2010)
SBTD05	3	2.235	110–130	0.531	0.492	0.396	Brinkman et al. (2010)
SBTD07	5	3.964	177–197	0.562	0.520	0.056	Brinkman et al. (2010)
T159S	3	3.000	195–211	0.685	0.658	0.377	Levine et al. (2000)
T27	4	3.742	275–287	0.403	0.437	0.082	Levine et al. (2000)
T7	2	2.000	219–227	0.407	0.470	0.053	Levine et al. (2000)

Alleles Number of Alleles. A_{52} Number of rarifacted alleles, *Allelic range* Range of Allele sizes, H_o Observed heterozygosity, H_s Expected heterozygosity averaged across subpopulations, *HWE* Probability of locus deviating from HWE expectations

study site. Using GenAlEx, we calculated probabilities of identity (PI and PI_{sib}); PI quantifies the probability of two unrelated individuals sharing identical genotypes, and PI_{sib} quantifies the probability of two related individuals sharing identical genotypes (Waits et al. 2001). PI was used to determine whether the number of markers used in the genotypes was sufficiently unique to minimize the risk of erroneously identifying two individuals as a single individual.

So as to examine the possibility of the Wahlund effect within our study sites, we used Genepop v4.0.10 (Raymond and Rousset 1995a) to test if genotype frequencies within populations met expectations of Hardy–Weinberg equilibrium (HWE) with the following parameters: 5,000 dememorization steps, 500 batches, with 5,000 iterations per batch. This test used a Markov-chain randomization test to estimate one–tailed *P*-values for each population at each locus (Guo and Thompson 1992). Across sites, *P*-values were combined using Fisher's method to analyze for population-wide departures from HWE in each locus. Fisher's method assumes that combined tests are independent, which we do not believe holds in this case because these study sites are in such close proximity that we would expect allele and genotype frequencies to be similar among them. Therefore, we used a false discovery rate (Benjamini and Yekutieli 2001) of 0.027 instead of $\alpha = 0.05$ as a critical threshold for hypothesis testing.

In order to quantify the neutral genetic diversity of our study sites, we used the program Fstat 2.9.3.2 (Goudet 2001) to characterize the genetic diversity within each locus by the number of alleles (*A*), alleles corrected for rarefaction (A_{52}) according to Mousadik and Petit (1996), the observed heterozygosity (H_o) and the expected heterozygosity averaged across sites (H_s). To examine for overall genetic population substructure, we utilized Fstat to calculate population sub-division (θ) following Weir and Cockerham (1984). Fstat was also used to test for linkage disequilibrium with Bonferroni correction for multiple comparisons (Rice 1989). We used Arlequin 3.5 (Excoffier and Lischer, 2010) to estimate inbreeding coefficients (F_{IS}) for each site and across all sites and to determine if the estimates were statistically significant using 10,000 permutations of data.

Genetic Differentiation

We performed a series of tests to identify the level of genetic differentiation among study sites, using multiple approaches to reduce the probability that any one family of approaches would produce misleading results. We used Fstat to perform an exact *G*-test to test for overall population subdivision (i.e., to reject overall panmixia), and the exact *G*-test in pairwise comparisons between sites, both tests based on 10,000 permutations (Goudet et al. 1995). Additionally, we used Genepop's genic pairwise population differentiation option and overall differentiation option, which both use Fisher's exact test of the *G* (log-likelihood ratio) statistic on a contingency table for each locus, using an unbiased estimation through a Markov-chain method using 5,000 dememorization steps, 500 batches with 5,000 iterations per batch (Raymond and Rousset 1995b).

Spatial autocorrelation and dispersal

We performed a spatial autocorrelation analysis using GenAlEx, which estimates mean relatedness (*r*, varying from −1 to 1) of all individuals with all other individuals within a certain distance category (Smouse and Peakall 1999). We used 9,999 permutations of data to create a 95 % confidence interval around a null hypothesis of $r = 0$ and 10,000 bootstraps to create a 95 % confidence interval around the mean estimate of *r*. We analyzed spatial autocorrelation by analyzing the three drainages separately and then combining the results, as recommended by Peakall et al. (2003) as a more conservative approach to estimating *r* than treating all individuals as if they came from a single population. We analyzed all individuals as well as males and females separately. We binned geographic distances in 500-m increments up to 4,000 m and in 1,000 m increments thereafter up to 7,000 m, which approximated the greatest distance between two individuals within a drainage. Distance bins were not cumulative, but rather were 500- or 1,000-m-wide bands. Estimates of *r* were plotted at the endpoint of each bin. We also analyzed local spatial autocorrelation by estimating mean *r* of individuals with their 5 nearest geographic neighbors, using 9,999 permutations of data to determine those observations that occurred in the upper and lower 2.5 % of the distribution (Double et al. 2005), representing significant positive and negative relatedness, respectively.

To determine if dispersal was sex-biased, we used GenAlEx to estimate assignment indices for every individual for the watershed in which it was found. Those indices were corrected (AIc) to a mean of zero by subtracting the mean from every individual assignment index and then were visualized in a histogram to determine if the distribution of indices had a long tail to the left, representing more extreme estimates of negative relatedness than positive and potentially representing dispersers (Favre et al. 1997; Mossman and Waser 1999). We tested for a sex bias in dispersal by testing for differences in means and variances of AIc between sexes for each site and across all sites using Fstat, which implements a *t* test for means and a permutation test (10,000 iterations) for variances. Because AIc was estimated using all individuals, means for each gender could be non-zero. We also tested for a sex bias in dispersal by comparing

Table 2 Population differentiation and migration between pairs of study sites

Location Pair (1/2)	θ	*P*-values for tests of population differentiation		$4N_em$ 1 → 2	$4N_em$ 2 → 1
		Fstat *G*-test	Genepop *G*-test		
Maybeso/Staney	0.015	0.017	0.004	25.91 (23.92–28.02)	3.73 (3.24–4.26)
Maybeso/Steelhead	0.0033	0.550	0.522	19.92 (18.0103–32.4044)	0.59 (0.4211–0.8061)
Steelhead/Staney	0.0049	0.050	0.075	4.83 (4.00–5.76)	9.17 (7.85–10.36)
Overall	0.0080	0.002	0.012		

The result of tests applied to location pairs, and over all locations. Mean estimates of $4N_em$ from Migrate-N allowing for asymmetric dispersal, with the 95 % confidence interval in parentheses

correlograms of spatial autocorrelation between the genders (Banks and Peakall 2012). In this case, we combined individuals from all three drainages into a single population for each gender. The two subsequent populations (male and female) were subjected to spatial autocorrelation analysis as before and the statistic omega (ω) was calculated to determine if the two correlograms differed significantly across all distance classes. Omega represents the combined probabilities of t^2-statistics for testing differences in r between the two correlograms at each distance class [see Banks and Peakall (2012) for details].

We estimated effective number of migrants ($N - {}_em$) using Migrate-N 3.0.3 (Beerli 2008), a program to obtain a maximum likelihood estimate of dispersal rates and effective population size through a coalascent approach (Beerli and Felsenstein 1999). This method is superior to inferring effective migrants from F_{ST} at low levels of population differentiation (Waples 1998; Whitlock and McCauley 1999). For our analysis, we followed the Brownian-motion model using the maximum-likelihood inference strategy, recording 2,500,000 trees with a sampling increment of 50, and replicating each analysis 4 times with adaptive heating. F_{ST} was used as a starting parameter to estimate the effective dispersal parameter per generation ($4N_em$; Beerli and Felsenstein 1999, 2001; Beerli 2004, 2008). The analysis was repeated with a variety of parameters to ensure convergence.

Results

During the sampling period, we collected 170 samples from the Staney watershed, 108 samples from Maybeso watershed and 98 samples from Steelhead watershed, for a total of 376 samples (Table 2). We were able to successfully amplify multilocus genotypes for 335 of these samples. Through mutlilocus matching, we identified 101, 52, and 68 individual deer in Staney, Maybeso, and Steelhead, respectively. Only 2 % of pairwise genotype comparisons were mismatched at 1 or 2 loci, indicating a very low chance of error when identifying individuals. Of those 221 individuals, we were able to determine gender for 141: 100 females and 41 males.

Genetic Diversity

Among the eight loci, there were between two (T7 and C89) and seven (SBTD04) alleles per locus ($\bar{x} = 3.6$ SD = 1.7). Our rarefacted number of alleles (A_{52}) ranged from 2.0 to 5.7 ($\bar{x} = 3.1$ SD = 1.3). Grouping all study sites, PI and PI_{sib} were 1.2×10^{-4} and 1.3×10^{-2}, respectively, using the 8 microsattelite loci, and were 7.1×10^{-5} and 1.0×10^{-2}, respectively, when adding the gender marker. Heterozygosity ranged between 0.199 (C89) and 0.658 (T159S) with an overall H_o of 0.492 (Table 1). We observed two instances of a locus being out of HWE in a study site. Locus SBTD06 did not conform to HWE in Staney ($P = 0.0052$) and locus T7 was not in equilibrium in Maybeso ($P = 0.018$). Nonetheless, no locus was significantly out of HWE when combined across sites (Table 1). No locus showed signs of linkage with other loci when corrected for multiple comparisons. Site-specific inbreeding coefficients were −0.042 for Steelhead, 0.006 for Staney and 0.030 for Maybeso; none were significantly different from zero ($P \geq 0.29$). Overall F_{IS} was −0.004, which also was not significant ($P = 0.56$).

Genetic differentiation

Pairwise θ values varied from 0.0033 to 0.0146 (Table 2) with an overall θ of 0.008. The exact *G*-test indicated population subdivision overall ($P = 0.002$) and we identified pairwise population subdivision between Maybeso/Staney ($P = 0.017$; Table 2) and Staney/Steelhead ($P = 0.050$). Fisher's exact test on a contingency table for overall population genetic differentiation indicated population structure ($P = 0.012$) among study sites; Maybeso/Staney were again found to differ ($P = 0.004$) although Steelhead/Staney did not ($P = 0.074$; Table 2). As Maybeso and Staney are the two most separated drainages we tested for the presence of isolation by distance, which

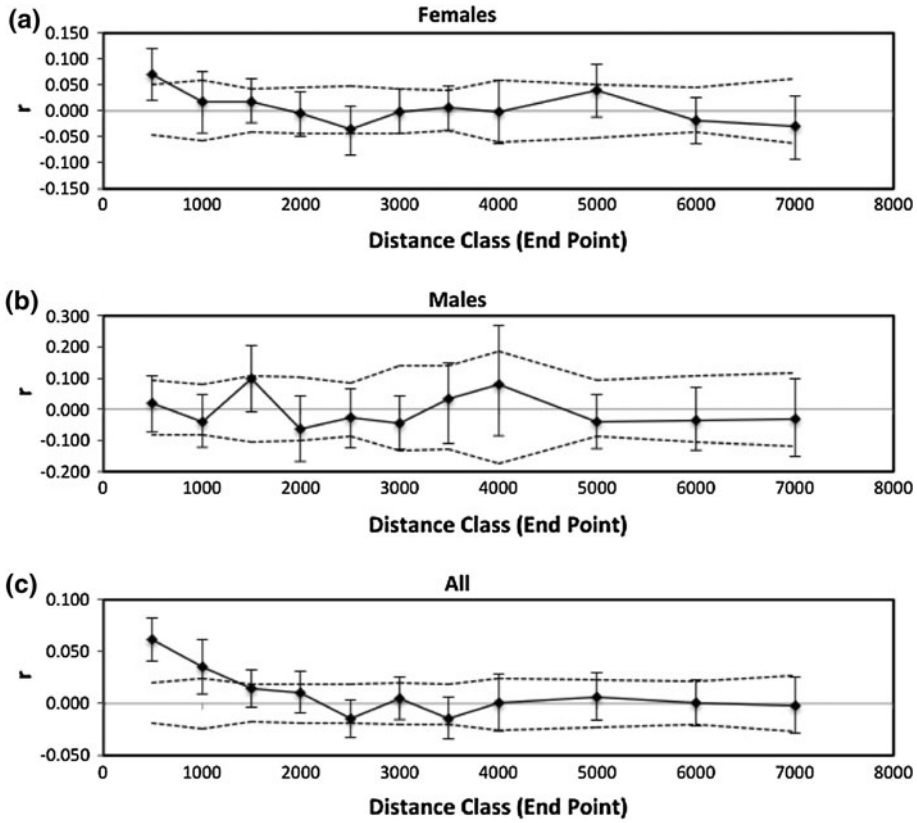

Fig. 2 Correlograms indicating degree of spatial autocorrelation at various distance classes for **a** all individuals, **b** females, and **c** males for Sitka black-tailed deer on Prince of Wales Island, Alaska, USA. *Distance classes* represent 500-m bins up to 4,000-m and 1,000-m bins thereafter. *Dashed lines* represent the 95 % confidence interval around a null hypothesis of $r = 0$. Estimates of r for each distance class are bounded by 95 % confidence intervals. *Arrows* indicate estimates of r that are significantly different from zero ($P < 0.05$)

we found using a Mantel test on individual genotypes ($r = 0.03$, $P = 0.045$).

Spatial autocorrelation and dispersal

When analyzing all individuals, significant positive relatedness was observed among individuals between 0 and 500 m ($r = 0.061$, $P < 0.001$) and between 501 and 1,000 m ($r = 0.035$, $P = 0.002$) (Fig. 2). Females demonstrated significant spatial autocorrelation, with animals within 500 m of each other having mean relatedness significantly greater than zero ($r = 0.071$, $P = 0.002$) (Fig. 2). For males, no autocorrelation was observed within 1,000 m but the estimate at 1,500 m was significantly positive ($r = 0.09$, $P = 0.04$) (Fig. 2).

Of 221 deer analyzed, 28 were significantly positively related to their 5 nearest neighbors ($P \leq 0.025$). Of those 28, 18 were of known sex; 14 were female and 4 were male. That sex ratio does not differ from the overall sample sex ratio ($\chi^2 = 0.49$, $P = 0.48$). Eight deer were significantly negatively related to their 5 nearest neighbors ($P \leq 0.025$), which could indicate dispersers. Seven of those were of known sex, with 4 being female and 3 being male, which also did not differ from the sample sex ratio ($\chi^2 = 0.54$, $P = 0.46$). Mean relatedness of a female to her 5 nearest female neighbors was 0.024 (SE = 0.015) whereas mean relatedness of a male to his 5 nearest male neighbors was -0.018 (SE = 0.017). Those means differ significantly ($t = 1.87$, $P = 0.033$). Thirteen females were significantly ($P < 0.05$) related to their 5 nearest female neighbors with mean $r = 0.25$. Mean relatedness for all other females with their 5 nearest female neighbors was -0.0096, which did not differ significantly from zero (z-test, $P = 0.77$). One male was significantly related to its 5 nearest male neighbors ($r = 0.23$).

Distributions of corrected assignment indices have long tails for negative values in all 3 watersheds and overall (Fig. 3), indicating the presence of potential dispersers. Males are present in those tails in all study sites and females are included in 2 of 3 study sites. Although mean AIc for females was always positive and mean AIc for males was always negative, we found no significant differences between the sexes for means or variances of AIc (Table 3). Gender-specific correlograms were not statistically significantly different (pairwise $\omega = 16.72$, $P = 0.78$).

Estimates of $4N_em$ (Table 2) varied between 0.59 (Steelhead to Maybeso) to 25.92 (Maybeso to Staney). Connectivity was generally low with the largest number of migrants potentially being sourced in Maybeso drainage. Assuming a generation time of 3 years, these estimates represent a rate of 2.2 effective migrants per year to 0.05 effective migrants per year.

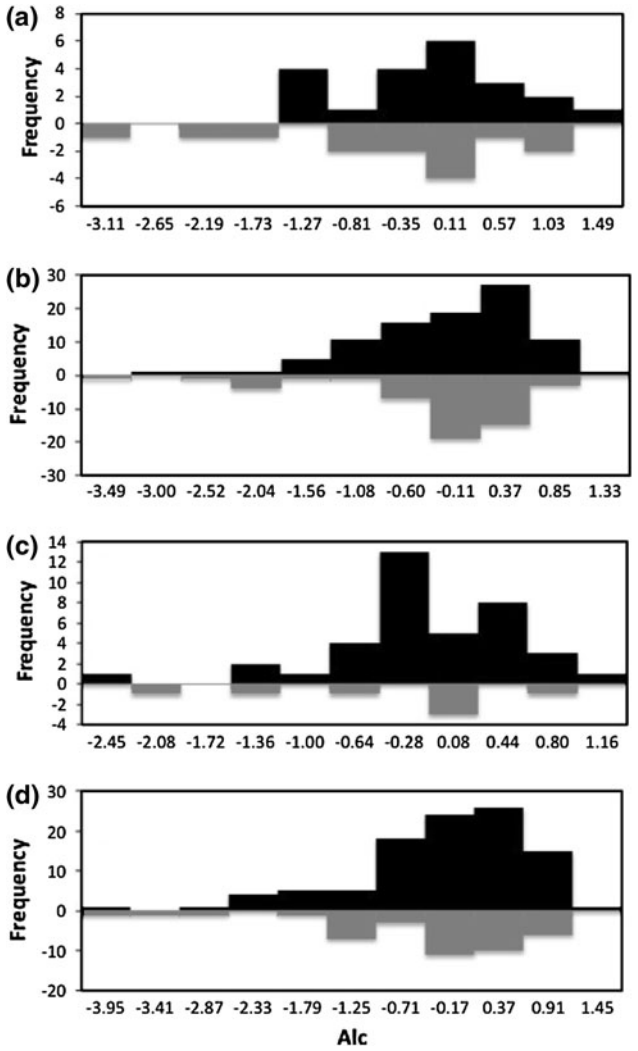

Fig. 3 Distributions of corrected assignment indices (AIc) for Sitka black-tailed deer of known gender in three watersheds: **a** Maybeso, **b** Staney, **c** Steelhead, and **d** overall on Prince of Wales Island, Alaska, USA. AIc for females (*black*) and males (*gray*) is shown. Axes are not the same scale

Discussion

We have confirmed the low level of genetic diversity present in this subspecies, documented previously by Latch et al. (2008), despite using different markers. The level of diversity found in SBTD on Prince of Wales Island is comparable to levels of diversity found in species considered threatened, or species thought to be at-risk due to extremely low diversity, as was previously reported by Latch et al. (2008). Although our results are not directly comparable because we used different microsatellites, our measurement of overall H_o was greater than the value of 0.401 found by Latch et al. (2008) for Prince of Wales Island. Latch et al. found other, lower observed heterozygosities throughout SBTD range, such as 0.403 in the Kodiak Archipelago, and 0.173 on Admiralty Island, Alaska. Using the same makers as this study, Chichagof Island, Alaska has an observed heterozygosity of 0.232 (K. Colson, unpublished data). However, diversity within our sampled populations still appears very low for a non-endangered mammal. Unlike the findings of Latch et al. (2008), our F_{IS} estimates were not indicative of population-wide heterozygote deficiency in SBTD on Prince of Wales Island. We do not possess evidence that SBTD are less fit due to their low heterozygosity and allelic diversity; however, their low diversity may reflect a lower potential to adapt to future challenges (Frankham et al. 1999, 2002). This low level of diversity may be due to an ancient bottleneck dating to the origination of the subspecies (Latch et al. 2009).

Whereas Latch et al. (2008) found population structure among islands, our study provides the first evidence that there is intra-island population structure in SBTD. We documented fine-scale population structure at the level of the watershed, which likely is a function of isolation by distance due to limted dispersal among watersheds. Although values of F_{ST} were small, they were statistically significant and were of the same magnitude as those estimated for other cervids exhibiting population structure (Nussey et al. 2005, Pérez-Espona 2008).

Other, sophisticated methods of identifying discrete populations exist. We attempted to examine genetic population structure using the Baysian assignment package Structure (Pritchard et al. 2000), which solved for a single genetic cluster (data not shown). However, Structure's traditional models are known to perform very poorly at low values of F_{ST} (Latch et al. 2006; Pritchard et al. 2010) such as the those found in our study area, so such analyses are beyond the reasonable capabilities of the software.

We also documented social structure among females, which tend to be related to those females living nearby, whereas males do not exhibit this structure. We believe that this is a function of fine-scale dispersal patterns, in which we hypothesize that, although both sexes are capable of dispersing, male dispersal distances that likely are greater than those of females. Male dispersal distances, however, may not be great enough to exit the watershed.

The number of effective migrants seems to reflect a very low rate of dispersal between watersheds,. Schoen and Kirchhoff (1985) observed only one dispersal event out of 51 radio-collared SBTD on Admiralty Island, Alaska. Our own results on Prince of Wales Island seem to support dispersal of SBTD being limited in frequency or distance. That observation is supported by the spatial scale of autocorrelation within study sites, which was on the order of 1,000 m.

Our results appear to provide some support for the rose-petal model (Porter et al. 1991) of female social structure in SBTD, where females tend to establish home ranges

Table 3 Mean and variance of corrected assignment index (AICc) for sexes of Sitka black-tailed deer for three study sites and overall, and significance levels for *t*-tests (means) and permutation tests (variances)

P-values are for one-tailed tests of hypotheses that males would have the lesser mean and greater variance

	Maybeso	Staney	Steelhead	Overall
Mean (*n*)				
Females	0.378 (21)	0.042 (40)	0.021 (39)	0.105 (100)
Males	−0.567 (14)	−0.085 (20)	−0.117 (7)	−0.255 (41)
P	0.13	0.41	0.43	0.19
Variance				
Females	3.01	6.40	2.89	4.34
Males	6.96	3.45	6.30	5.18
P	0.12	0.83	0.059	0.36

adjacent to their natal range. The 0–500 m distance class is similar in magnitude to the mean maximal recapture distance in those populations ($\bar{x} = 443$ m, SE = 61.0; Brinkman et al. 2011), which may serve as an estimate of home range extent. Thus, the significantly elevated relatedness occurs within 1 home range distance of the comparison individual and females appear to have adjacent or overlapping home ranges to related individuals.

Fine-scale genetic structure on the scale of hundreds of meters has been found in other cervid populations recently, both managed (Miller et al. 2010; Cullingham et al. 2011) and unmanaged (Nussey et al. 2005), indicating that this scale of social structure is fairly common. Nonetheless, Lang and Blanchong (2012) found genetic structure in white-tailed deer out to a distance of 29 km. Moreover, presence of matrilineal social groups seems to be dependent on an extended age structure and the presence of mature, dominant, females (Aycrigg and Porter 1997), which is inconsistent with populations that are hunted. Indeed, Comer et al. (2005) found very weak female social structure in a heavily hunted population of white-tailed deer. Female SBTD on Prince of Wales Island are not legal to hunt, which may contribute to the presence of structure.

Estimates of relatedness in the smallest distance class (0–500 m) likely are biased high because we could not avoid comparisons between a female and any fawns-of-the-year that may have accompanied her. As those individuals are not independent, those comparisons ideally should be eliminated from the data. Nonetheless, we do not believe that our findings are governed solely by this. For those females significantly related to their 5 nearest female neighbors, mean relatedness was 0.25, meaning that on average each of those 5 females are 2 levels of consanguinity removed from the focal female (i.e., grandmothers or granddaughters). As a female deer can have no more than 2 fawns at a time and assuming that only those fawns-of-the-year have lacked an opportunity to disperse, a group of 5 female neighbors including 2 female fawns and 3 unrelated individuals with a mean relatedness to the focal individual of zero would yield an expected overall relatedness value of 0.2. This would be the worst-case scenario for the effect of female fawns inflating relatedness values if there were indeed no spatial structure; yet, females with 2 surviving daughters in early spring would be a relatively unusual event. That combination would only occur in 1 out of 4 sets of twins by chance and deer fawns in our study area have experienced ~80 % mortality rates due to predation and severe winter weather similar to the weather experienced during the winter prior to our data collection (Alaska Department of Fish and Game, unpublished data). Understandably, we believe that under prevailing predation rates and weather conditions the relative abundance of female twins in early spring would be very low; therefore, female fawns accompanying adult females is not the most parsimonious explanation for our significant estimates of relatedness for a female and her 5 nearest female neighbors.

Unfortunately, a parentage test would not be informative about identifying fawns—at-heel of the focal deer. We cannot distinguish between adult daughters or the dam of the focal deer that have nearby home ranges versus female fawns-at-heel that have yet to disperse because they are still dependent on the dam. This caveat may also apply to full-sib sisters of the focal deer.

Our results would also be confounded by seasonal movements by deer, which have been documented in radio-telemetry studies in southeastern Alaska, indicating a migratory component of some populations (Schoen and Kirchhoff 1990). Migratory deer only occur in watersheds with abundant alpine habitat (Alaska Department of Fish and Game, unpublished data), which characterized the Maybeso watershed but not the two others in this study. Nonetheless, it is possible that heavy snows can force deer living at higher elevations in summer, though not in alpine habitats, to move to lower elevations in winter to escape the snow burden. This would have the same effect on our study area as would migratory deer, i.e., non-resident deer living in the area seasonally. Given that we have documented female social structure in this population while on winter range, it may be possible that matrilineal groups do not permit non-resident deer to inhabit areas that the matrilineal group does, which would serve to maintain the

structure we observed. Additionally, it is possible that matrilineal groups that migrate may maintain cohesion and take up residence on winter range in close proximity. That behaviour has been observed in white-tailed deer in New York (Mathews and Porter 1993).

With dispersal being sex-biased primarily in favor of males in Columbian black-tailed deer (*O. h. columbianus*; Bunnell and Harestad 1983), it is likely that in SBTD the relatively few effective migrants between populations are primarily male, and the watersheds therefore would be demographically independent. Both males and females demonstrate some degree of dispersal within our study area; however, only females demonstrated fine-scale structure, which suggests that female dispersal may be less than levels of dispersal found in males, or that females disperse shorter distances than males. Our study area was typical of SBTD habitat in managed forest in southeastern Alaska and there is no reason to expect that population structure does not occur on similar spatial scales elsewhere. Based on this reasoning, it appears evident that SBTD are not a single, panmictic, population on Prince of Wales Island, but exist in multiple populations of varying demographic independence.

Sex-biased dispersal is difficult to detect genetically and the power of the test depends on the characteristics of dispersal. Goudet et al. (2002) showed that unless dispersal is heavily skewed toward one gender and that dispersal rates are high, techniques such as AIc cannot detect differences between genders. This actually supports our conclusions, however. If deer truly had highly sex-biased dispersal rates or dispersed at high rates in general, the tests we implemented would be more likely to detect those events.

Additional research is necessary to understnad the frequency and distance of dispersal in both sexes. We cannot discount isolation by distance as a driver of population structure, despite the separation between the two most distant watersheds being only 44 km. Mean dispersal distance of male Columbian black-tailed deer on Vancouver island was observed by Bunnell and Harestad (1983) to be 5.6 ± 1.7 km, far less than the distance between our two closest study sites. Long distance dispersal events are thought in part to simply be dispersers having to travel farther to reach suitable habitats (Linnell et al. 1998), and the proximity of available habitat would limit the number of long distance dispersals. On Prince of Wales Island, male deer suffer high mortality rates due to predation and hunting, which likely create openings that can be exploited by dispersing yearlings. Nearby open habitat within a watershed would favor short-distance dispersals, and the formation of population subdivision, yet cause dispersion of males to the point that they do not display fine-scale structure compared with females. Long et al. (2008) demonstrated that dispersal distance in male white-tailed deer may be related to social structure in the population, and we hypothesize that a similar mechanism may operate in SBTD when males suffer high mortality rates, such as under intensive harvest regimes.

Of the 6 rates of effective dispersal between watersheds that we estimated, the two highest were those with Maybeso as the source. Although the estimate for Maybeso to Staney (the most distant watersheds) was greater than that for Maybeso to Steelhead, the 95 % confidence interval of Maybeso-to-Staney was contained within that for Maybeso-to-Steelhead, indicating no significant difference. The two lowest estimates of migration rates were those with Maybeso as the receiving population. The primary inference from those data is that Maybeso is a source for dispersing deer compared to the other two drainages and it receives few migrants in return. Reasons behind this remain unclear but we do note that the primary difference between Maybeso versus Steelhead and Staney is that Maybeso is composed of older second-growth stands that yield lower harvest rates for hunters (Brinkman et al. 2007).

Other factors driving population subdivision may involve the role of snow at high elevation in constraining movement (Klein and Olson 1960; Schoen and Kirchhoff 1985). Snowfall is linked with increased energetic expenditure in SBTD, more so than the increase in the energetic expenditure from cold temperature (Parker et al. 1999). Deer winter ranges occur at significantly lower elevations in high snow years (Schoen and Kirchhoff 1990). However, it is impossible to infer what the most significant barriers to dispersal are from this study alone. Further investigation is required to find the role of disturbance, habitat, harvest, predation, and geographic factors in the development of population structure in SBTD.

Our study suggests that SBTD exist in a fine-scale mosaic of populations even within a single island. Dispersal appears to be limited, with females establishing home ranges adjacent to their natal areas and males likely remaining in or near the watershed of their birth. Although it would be impractical to manage SBTD on a per-watershed basis, future management should be cognizant of potential fine-scale population structure, especially when considering topographically complex areas recovering from low population sizes, as immigration may be an ineffective means to increase abundance.

Acknowledgments Support was provided by the Alaska Department of Fish and Game and the USDA Forest Service. Funding was provided by the USDA Forest Service, Alaska Trappers Association, the University of Alaska Fairbanks Resilience and Adaptation Program (IGERT, NSF 0114423), Pacific Northwest Research Station grant PNW01-JV11261952-231, the Bonanza Creek LTER (NSF 0423442), and the University of Alaska Fairbanks Institute of Arctic Biology. We acknowledge Hydaburg Cooperative Association for providing field assistance, especially J. Adams, A. Peratrovich, and T. Christianson. R. Janzen, A. Nelson, N. Phillips, and N. Swensgard provided data collection and analysis assistance. We thank S. Turner for comments on earlier drafts of this manucsript.

References

Alaback PB (1982) Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. Ecology 63: 1932–1948

Allendorf FW, Luikart G (2006) Conservation and the genetics of populations. Blackwell Publishing, Oxford

Anthony LL, Blumstein DT (2000) Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce N_e. Biol Conserv 3:303–315

Aycrigg JL, Porter WF (1997) Sociospatial dynamics of white-tailed deer in the Central Adriondack Mountains, New York. J Mamm 78:468–482

Banks SC, Peakall R (2012) Genetic spatial autocorrelation can readily detect sex-biased dispersal. Mol Ecol 21:2092–2105

Beerli P (2004) Effect of unstapled populations on estimation of population sizes and migration rates between sampled populations. Mol Ecol 13:827–837

Beerli P (2008) Migrate version 3.0—a maximum likelihood and Bayesian estimator of gene flow using the coalescent. Distributed over the Internet at http://popgen.scs.edu/migrate.html

Beerli P, Felsenstein J (1999) Maximum likelihood estimation of migration rates and population numbers of two populations using a coalescent approach. Genetics 13:763–773

Beerli P, Felsenstein J (2001) Maximum likelihood estimation of migration rates and population numbers of two populations using a coalescent approach. Proc Natl Acad Sci USA 98:4563–4568

Bellemain E, Swenson JE, Tallmon D, Brunberg S, Taberlet P (2005) Estimating population size of elusive animals with DNA from hunter-collected feces: four methods for brown bears. Conserv Biol 19:150–161

Benjamini Y, Yekutieli D (2001) The control of the false discovery rate in multiple testing under dependency. Ann Stat 29:1165–1188

Brinkman TJ, Hundertmark KJ (2009) Sex identification of northern ungulates using low quality and quantity DNA. Conserv Genet 10:1189–1193

Brinkman TJ, Kofinas GP, Chapin FS III, Person DK (2007) Influence of hunter adaptability on resilience of subsistence hunting systems. J Ecol Anthr 11:58–63

Brinkman TJ, Person DK, Schwartz MK, Pilgrim KL, Colson KE, Hundertmark KJ (2010) Individual identification of Sitka black-tailed deer (Odocoileus hemionus sitkensis) using DNA from fecal pellets. Conserv Genet Resour 2:115–118

Brinkman TJ, Person DK, Chapin FS III, Smith W, Hundertmark KJ (2011) Estimating abundance of Sitka black-tailed deer using DNA from fecal pellets. J Wildl Manag 75:232–242

Brown JL (1997) A theory of mate choice based on heterozygosity. Behav Ecol 8:60–65

Bunnell FL, Harestad AS (1983) Dispersal and dispersion of black-tailed deer: models and observations. J Mammal 64:201–209

Chang KT, Verbyla DL, Yeo JJ (1995) Spatial analysis of habitat selection by Sitka black-tailed deer in southeast Alaska. J Environ Manag 19:579–589

Coltman DW, Pilkington JG, Pemberton JM (2003) Fine-scale genetic structure in a free-living ungulate population. Mol Ecol 12:723–742

Comer CE, Kilgo JC, D'Angelo GJ, Glenn TC, Miller KV (2005) Fine-scale genetic structure and social organization in female white-tailed deer. J Wildl Manag 69:332–344

Cullingham CI, Merrill EH, Pybus MJ, Bollinger TK, Wilson GA, Coltman DW (2011) Broad and fine-scale genetic analysis of white-tailed deer populations: estimating the relative risk of chronic wasting disease spread. Evol Appl 4:116–131

Double MC, Peakall R, Beck NR, Cockburn A (2005) Dispersal, philopatry and infidelity: dissecting local genetic structure in superb fairy-wrens. Evolution 59:625–635

Excoffier L, Lischer HEL (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Mol Ecol Resour 10:564–567

Farmer CJ, Person DK, Bowyer RT (2006) Risk factors and mortality of black-tailed deer in a managed forest landscape. J Wildl Manag 70:1403–1415

Favre L, Balloux F, Goudet J, Perrin N (1997) Female-biased dispersal in the monogamous mammal *Crocidura russula*, evidence from field data and microsatellite patterns. Proc R Soc Lond B Biol Sci 264:127–132

Frankham R, Lees K, Montgomery ME, England PR, Lowe EH, Briscoe DA (1999) Do population size bottlenecks reduce evolutionary potential? Anim Conserv 4:255–260

Frankham R, Ballou JD, Briscoe DA (2002) Introduction to conservation genetics. Cambridge University Press, Cambridge

Goudet J (1995) FSTAT v1.2. A computer program to calculate F-statistics. J Hereditary 86:485–486

Goudet J (2001) FSTAT, a program to estimate and test gene diversities and fixation indices. Version 2.9.3 Available from http://www2.unil.ch/popgen/softwares/fstat.htm

Guo SW, Thompson EA (1992) Performing the exact test of Hardy–Weinberg proportions for multiple alleles. Biometrics 48:361–372

Hanley TA (1993) Balancing economic development, biological conservation, and human culture: the Sitka black-tailed deer Odocoileus hemionus sitkens is as an ecological indicator. Biol Conserv 66:61–67

Hartl GB, Lang G, Klein F, Willing R (1991) Relationships between allozymes, heterozygosity and morphological characters in red deer (Cervus elaphus), and the influence of selective hunting on allele frequency distributions. Heredity 66:343–350

Hedrick PW, Kim TJ, Parker KM (2001) Parasite resistance and genetic variation in the endangered Gila topminnow. Anim Conserv 4:103–109

Kirchhoff MD, Pitcher KW (1990) Evaluation of methods for assessing deer population tends in Southeast Alaska. Alaska Department of Fish and Game Research Report. On File: ADFG Wildlife Conservation, Douglas, AK 99824

Klein DR, Olson ST (1960) Natural mortality patterns of deer in Southeast Alaska. J Wildl Manag 24:80–88

Kohn MH, Wayne RK (1997) Facts from feces revisited. Trends Ecol Evol 12:223–227

Lang KR, Blanchong JA (2012) Population genetic structure of white-tailed deer: understanding risk of chronic wasting disease spread. J Wildl Manag 76:832–840

Latch EK, Dharmarajan G, Glaubitz JC, Rhodes OE Jr (2006) Relative performance of Bayesian clustering software for inferring population substructure and individual assignment at low levels of population differentiation. Conserv Genet 7:295–302

Latch EK, Amann RP, Jacobson JP, Rhodes OE Jr (2008) Competing hypotheses for the etiology of cryptorchidism in Sitka black-tailed deer: an evaluation of evolutionary alternatives. Anim Conserv 11:234–246

Latch EK, Heffelfinger JR, Fike JA, Rhodes OE Jr (2009) Species-wide phylogeography of North American mule deer (Odocoileus hemionus): cryptic glacial refugia and postglacial recolonization. Mol Ecol 18:1730–1745

Levine K, Banks J, Sadowski G, Bienvenue P, Jones KC (2000) DNA-based markers in black-tailed and mule deer for forensic applications. Calif Fish Game 86:115–126

Linnell JDC, Wahlstrom K, Gaillard J-M (1998) From birth to independence: neonatal mortality, hiding behavior and dispersal. In: Andersen R, Duncan P, Linnell JDC (eds) The European roe deer: the biology of success. Scandinavian University Press, Oslo, pp 257–285

Long ES, Diefenbach DR, Rosenberry CS, Wallingford BD (2008) Multiple proximate and ultimate causes of natal dispersal in white-tailed deer. Behav Ecol 19:1235–1242

Mathews NE, Porter WF (1993) Effects of social structure on genetic structure of free-ranging white-tailed deer in the Adirondak mountains. J Mammal 74:33–43

Miller BF, DeYoung RW, Campbell TA, Laseter BR, Ford WM, Miller KV (2010) Fine-scale and genetic social structuring in a central Appalachian white-tailed deer herd. J Mammal 91: 681–689

Mills LS, Citta JJ, Lair KP, Schwartz MK, Tallmon DA (2000) Estimating animal abundance using noninvasive DNA sampling: promise and pitfalls. Ecol Appl 10:283–294

Mossman CA, Waser PM (1999) Genetic detection of sex-biased dispersal. Mol Ecol 8:1063–1067

Mousadik A, Petit RJ (1996) High level of genetic differentiation for allelic richness among populations of argan tree [*Argania spinosa* (L.) Skeels] endemic to Morocco. Theor Appl Genet 92:832–839

Nussey DH, Coltman DW, Coulson T, Kruuk LEB, Donald A, Morris SJ, Clutton-Brock TH, Pemberton J (2005) Rapidly declining fine-scale genetic structure in female red deer. Mol Ecol 14:3395–3405

Parker KL, Gillingham MP, Hanley TA, Robbins CT (1999) Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. Wildl Monogr 143:3–48

Peakall R, Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Mol Ecol Notes 6:288–295

Peakall R, Ruibal M, Lindenmayer DB (2003) Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes*. Evolution 57:1182–1195

Pérez-Espona S, Pérez-Barbería FJ, Mcleod JE, Jiggins CD, Gordon IJ, Pemberton JM (2008) Landscape features affect gene flow of Scotish Highland red deer (*Cervus elaphus*). Mol Ecol 17:981–996

Porter WF, Matthews NE, Underwood HB, Sage RW, Behrend DF (1991) Social organization in deer: implications for localized management. Environ Manag 15:809–814

Pritchard JK, Stephens M, Donnelly P (2000) Inferrence of population structure from multilocus genotype data. Genetics 155:945–959

Pritchard JK, Wen X, Falush D (2010). Documentation for STRUCTURE software: version 2.3. Available from http://pritch.bsd.uchicago.edu

Prugnolle F, Manica A, Balloux F (2005) Geography predicts neutral genetic diversity of human populations. Curr Biol 5:159–160

Raymond M, Rousset F (1995a) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. J Heredity 86:248–249

Raymond M, Rousset F (1995b) An exact text for population differentiation. Evolution 46:1280–1283

Rice WR (1989) Analysing tables of statistical tests. Evolution 43:223–225

Schoen JW, Kirchhoff MD (1985) Seasonal distribution and home-range patterns of Sitka black-tailed deer on Admiralty Island, southeast Alaska. J Wildl Manag 49:96–103

Schoen JW, Kirchhoff MD (1990) Seasonal habitat use by Sitka black-tailed deer on Admiralty Island, Alaska. J Wildl Manag 54:371–378

Smouse PE, Peakall R (1999) Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. Heredity 82:561–573

Taberlet P, Griffin S, Goossens B, Questlau S, Manceau V, Escaravage N, Wait LP, Bouvet J (1996) Reliable genotyping of samples with very low DNA quantities using PCR. Nucl Acids Res 24:3189–3194

Unit 2 Deer Planning Subcommittee (2005) Unit 2 deer management. Southeast Alaska Subsistence Regional Advisory Council. Anchorage, Alaska, USA

van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes 4:535–538

Waits LP, Luikart G, Taberlet P (2001) Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. Mol Ecol 10:249–256

Waples RS (1998) Separating the wheat from the chaff: Patterns of genetic differentiation in high gene flow species. J Heredity 89:438–450

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370

Whitlock MC, McCauley DE (1999) Indirect measures of gene flow and migration: $F_{ST} \neq 1/(4Nm + 1)$. J Heredity 82:117–125

Yeo JJ, Peek JM (1992) Habitat selection by female Sitka black-tailed deer in logged forests of southeastern Alaska. J Wildl Manag 56:253–261