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SPATIAL AND GENETIC ORGANIZATION OF THE ISLAND SPOTTED SKUNK, *SPILOGALE GRACILIS AMPHIALA*

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ABSTRACT—We assessed the spatial and genetic organization of the island spotted skunk (*Spilogale gracilis amphiala*) on Santa Cruz Island, California. Home ranges of adults were largely non-overlapping, consistent with expectations for a solitary species. Contrary to expectations, we found no evidence of a matrilineal spatial structure. Relatedness of adult females was not negatively correlated with geographic distance, nor was it positively correlated with overlap of home ranges, possibly because of excessive dispersal caused by exceptionally high densities. We did find evidence of a patrilineal structure at one study site, where relatedness among males was negatively correlated with distance. The explanation for differences between males and females in genetic structure is uncertain, but it may reflect the differential influence of high density on dispersal of males and females.

RESUMEN—Se evaluó la organización espacial y genética del zorrillo moteado (*Spilogale gracilis amphiala*) en la isla de Santa Cruz, California, USA. Los rangos de hogar de los adultos no fueron por lo general superpuestos, consistente con las expectativas de una especie solitaria. Contrariamente a lo esperado, no se encontró evidencia de una estructura espacial matrilineal. El parentesco entre las hembras adultas no se correlacionó negativamente con la distancia geográfica, ni tampoco se correlacionó positivamente con la superposición de los rangos de hogar, posiblemente debido a la dispersión excesiva causada por densidades excepcionalmente altas. Encontramos evidencia de una estructura patrilineal en un sitio de estudio, donde el parentesco entre machos se correlacionó negativamente con la distancia. La explicación de las diferencias entre machos y hembras en la estructura genética es incierta, pero puede reflejar la influencia diferencial de alta densidad en la dispersión de machos y hembras.

Mammals are characterized by a general pattern of female philopatry and male-biased dispersal and express varying degrees of sociality, from solitary to highly social (Greenwood, 1980; Dobson, 1982; Liberg and von

Schantz, 1985). Female philopatry is expected to generate spatial clusters of related females, which can result in the formation of social groups, and studies from a variety of mammalian species have documented that related fe-

males often live in close proximity (e.g., Armitage, 1996; McEachern et al., 2007).

Carnivores are no exception to this pattern (Gompper and Wayne, 1996; Ratnayeke et al., 2002), but they are on the less social end of the mammalian spectrum (Bekoff et al., 1984). Nonetheless, even solitary carnivores are expected to follow the typical mammalian pattern of females establishing home ranges close to their natal origins and often sharing space with female kin (Waser and Jones, 1983). Evaluating this expectation has been hindered by the difficulty of capturing solitary carnivores and monitoring them closely enough to observe their spatial movements and kin relationships (Ratnayeke et al., 2002). Moreover, of the few studies conducted, some have revealed that not all populations of carnivores follow the typical matrilineal pattern (Schenk et al., 1998; Schaeff et al., 1999; Blundell et al., 2004).

The western spotted skunk (*Spilogale gracilis*) is an elusive species, and little is known of its spatial or social organization (Dragoo, 2009). One subspecies, the island spotted skunk (*S. g. amphiala*), is restricted to two of the Channel Islands, Santa Cruz and Santa Rosa, off the coast of southern California. We used trapping, radiotelemetry, and genetic analysis of microsatellite variation to investigate spatial organization and its relationship with genetic relatedness in island spotted skunks on Santa Cruz Island. We hypothesized that the island spotted skunk would be solitary (Dragoo, 2009) and exhibit a matrilineal spatial structure resulting from female philopatry and male dispersal (Greenwood, 1980; Waser and Jones, 1983). We expected that relatedness would be negatively correlated with geographic distance for females but show no correlation for males, that neighboring skunks would show little overlap in space use (Bekoff et al. 1984), and that, because of the benefits of kin selection (Hamilton, 1996), same-sex pairs of neighboring skunks would be more likely to share space if they were more closely related.

Santa Cruz Island (34°0'N, 119°45'W) is located within Channel Islands National Park and lies 40 km off the mainland south of Santa Barbara, California. The island is ca. 3–11 km wide and 39 km long, with a total area of ca. 25,000 ha. Its climate is maritime Mediterranean, with pronounced wet (December–April) and dry (May–November) seasons. Research on the island was conducted from August 2003–September 2004 at two sites 7.5 km apart. The site at Valley Anchorage (370 ha), located at the eastern end of the Central Valley of the island, was characterized by open grassland, coastal sage scrub, and chaparral. The site at Willows Drainage (410 ha), located on the southern side of the island, had steeper topography and more barren slopes and supported mostly open grassland and chaparral, with little coastal sage scrub.

Adult skunks were live-trapped in Tomahawk single-door box traps placed throughout each study site. We

attempted to capture all skunks at Valley Anchorage via repeated trapping throughout the site, but we may have missed some skunks at Willows Drainage because of lower intensity of trapping and inaccessibility of some areas. We collected a 2-mm biopsy of tissue from an ear of each skunk and stored the sample in 95% ethanol for subsequent genetic analysis. We fitted 40 skunks with radio-collars (Holohil Systems, Carp, Ontario). Island spotted skunks are nocturnal, so we determined spatial locations of skunks using a combination of radiotelemetric triangulation during the night, radiotelemetric homing on skunks in dens during the day, and locations of traps in which skunks were captured. Details of methods of trapping and radiotelemetry are provided in Jones et al. (2008).

We used Ranges 6 (Kenward et al., 2003) to determine spacing of centers of ranges and overlap of home ranges between skunks. For each skunk, we determined a range-center using the harmonic mean of all locations; for individuals known only from their initial capture, the location of the trap was used as their range-center. We used the 95%-fixed-kernel method, with least squares cross-validation, to calculate annual home ranges for those skunks with ≥ 25 locations, with each location separated by ≥ 4 h. We then determined the percentage of overlap of home range for all adults with overlapping or adjacent home ranges, with a modification of Cole's coefficient of association (Kenward, 2001): coefficient of overlap = $2 \times (\text{Overlap}_1 \times \text{Area}_1) / (\text{Area}_1 + \text{Area}_2)$, where the home-range area_x of skunk x has a proportion of overlap_x. Because data were not normally distributed, we used nonparametric tests in JMP (version 4.0; SAS Institute Inc., Cary, North Carolina) to assess the effect of site (Wilcoxon rank sums test) and dyad type (male–male, female–male, and female–female; Kruskal–Wallis nonparametric one-way analysis of variance) on overlap of home range. These nonparametric results should be interpreted with caution due to lack of independence among measures of overlap (i.e., some skunks were represented in multiple dyads).

Genomic DNA was extracted from samples of tissue from ears using either the Qiagen DNeasy 96 Tissue Kit or the Promega Wizard SV 96 Genomic DNA Purification System. We then examined genotypes at the eight microsatellite loci described by Floyd et al. (2011) except for rTt-2, for which our skunks were monomorphic. Polymerase chain-reaction (PCR) amplifications were made in 10- μ L reactions (0.5–1.0 ng/ μ L DNA, 1X Roche FastStart *Taq* buffer, 0.05 units/ μ L Roche FastStart *Taq* DNA polymerase, 2–3 mM MgCl₂, 0.16–0.2 mM dNTPs, 0.1 μ g/ μ L BSA, and 0.25–0.5 μ M of each primer) on either an MJ Research, Inc PTC-100 or a DNA Engine Dyad thermocycler. Conditions for amplification began with 4 min at 95°C, followed by 40 cycles of denaturing for 30 s at 95°C, annealing for 25–35 s at 50–55°C, and extending for 30 s to 1 min at 72°C, with a final extension

of 10–30 min at 72°C. Products resulting from PCR were diluted with 10–30 μ L of 98%-formamide loading buffer, denatured for 6 min at 92°C, separated on 5% denaturing polyacrylamide gels, stained with fluorescent dye, and visualized with a Molecular Dynamics FluorImager 595.

For the microsatellite data, Bonferroni-corrected tests for Hardy–Weinberg equilibrium and linkage disequilibrium were conducted using GENEPOP 4.0 (Raymond and Rousset, 1995). After utilizing CONVERT 1.31 (Glaubitz, 2004) to convert the data files, STRUCTURE 2.2 (Pritchard et al., 2000) was used to confirm that both study sites represented the same single interbreeding population; all subsequent analyses treated them as such. Because STRUCTURE assumes Hardy–Weinberg equilibrium, we also did the analysis without the locus that failed to meet this assumption (Lut832), but a single population was still indicated. Finally, pairwise-relatedness-coefficients that did not assume Hardy–Weinberg equilibrium (Queller and Goodnight, 1989) for all possible pairings of skunks were generated using SPAGeDi 1.2 (Hardy and Vekemans, 2002). Relatedness coefficients range from 1 for genetically identical individuals to 0 for unrelated individuals, although negative values can occur when individuals are less related than random individuals (Hardy and Vekemans, 2002).

We used range-centers to calculate pairwise geographic distances between skunks. To assess correlations between relatedness and geographic distance, Mantel tests (Mantel, 1967) in XLSTAT (version 2008.5.01, Addinsoft, New York, New York) were conducted using the Pearson correlation coefficient and 10,000 permutations. To assess correlations between overlap of home ranges and relatedness, use of the Mantel test was precluded because of missing cells or nonsquare matrices. Hence, we first used Spearman's rank correlation to measure the degree of association between the two variables. We then tested the null hypothesis of no significant correlation with a nonparametric permutation test in Resampling Stats for Excel (version 3.2, Resampling Stats, Inc., Arlington, Virginia), using 10,000 iterations (Ratneyeke et al., 2002; Stoen et al., 2005).

We trapped 115 adult skunks (85 males, 30 females) and had sufficient radiotelemetric locations to delineate home ranges for 27 skunks (14 males, 13 females). Coefficients of overlap of home ranges for adults ranged from 0.0–69.1%, with a mean of 22.8% ($SE = 2.21$, $n = 90$). Mean overlap was 24.7% for male–male dyads ($SE = 3.42$, $n = 38$), 19.5% for female–female dyads ($SE = 7.97$, $n = 7$), and 21.7% for male–female dyads ($SE = 3.14$, $n = 45$). We found no significant effects of site ($\chi^2 = 1.57$, $df = 1$, $P = 0.21$) or dyad type ($\chi^2 = 1.75$, $df = 2$, $P = 0.42$) on overlap of home ranges.

Genetic analyses included all 115 individuals, with missing genotype data averaging 1%. No linkage disequilibrium was found (21 tests, $P \geq 0.05$); however, one locus (Lut832) was not in Hardy–Weinberg equilibrium

($P < 0.01$). Observed heterozygosities for loci ranged from 0.348–0.704, with a mean of 0.556. The mean relatedness among all individuals was -0.01 ($SD = 0.345$, $n = 3,489$ dyads) within study sites and -0.02 ($SD = 0.338$, $n = 3,066$) between sites. Mean relatedness within sites was 0.00 for male–male dyads ($SD = 0.353$, $n = 1,887$), -0.04 for female–female dyads ($SD = 0.325$, $n = 238$), and -0.02 for male–female dyads ($SD = 0.337$, $n = 1,364$).

We found no significant correlation between relatedness and geographic distance for females at Valley Anchorage ($r = -0.04$, $P = 0.54$, $n = 210$) and Willows Drainage ($r = -0.01$, $P = 0.97$, $n = 28$), even when females from the two sites were combined to increase the spatial scale and improve statistical power ($r = 0.03$, $P = 0.58$, $n = 406$). Males at Willows Drainage also showed no significant correlation ($r = 0.01$, $P = 0.85$, $n = 561$), but the correlation was significantly negative for males at Valley Anchorage ($r = -0.11$, $P < 0.01$, $n = 1,326$). We found no significant correlation between relatedness and overlap of home ranges for males at Valley Anchorage ($r = -0.21$, $P = 0.32$, $n = 23$) and at Willows Drainage ($r = 0.04$, $P = 0.88$, $n = 15$) or for females when data were combined for both sites to improve statistical power ($r = 0.02$, $P = 1.00$, $n = 7$).

Mammals on islands might show a number of demographic and behavioral differences compared with mainland species, including higher densities, constrained dispersal, and increased overlap between adjacent territories (Stamps and Buechner, 1985; Adler and Levins, 1994). Island spotted skunks expressed at least one of those characteristics, with densities of populations at Valley Anchorage (19 adults/km²) and Willows Drainage (9 adults/km²) that were extraordinarily high for carnivores (Jones et al., 2008). The skunks we captured exhibited a sex ratio biased toward males. A male bias for captured skunks has been reported previously for Santa Cruz Island (Crooks et al., 2003) and for mainland spotted skunks as well (Doty and Dowler, 2006) and might reflect differential trappability instead of a biased sex ratio in the population (Doty and Dowler, 2006). Consequently, actual densities of adults at our study sites might have been even higher.

Our estimates of overlap of home ranges for island spotted skunks are consistent with expectations and indicate that home ranges of neighboring pairs of adults are largely non-overlapping. However, our mean overlap (23%) is toward the upper end of the range of values reported for other solitary mammals (5–31%; Oli et al., 2002; Burton and Krebs, 2003; Innes et al., 2009; Maher, 2009; Jesmer et al., 2011). Further, we did not radio-track all skunks at each study site. Consequently, actual overlap among skunks may have been somewhat higher, perhaps reflecting the pattern of increased territorial overlap thought to be a characteristic of island vertebrates (Stamps and Buechner, 1985).

The spatial clustering of related females is well known for social mammals, but recent research has revealed that an association between spatial proximity and relatedness also may occur in solitary species because of female philopatry (Ratnayeke et al., 2002; McEachern et al., 2007; Maher, 2009), with females more likely to share space with relatives (Ratnayeke et al., 2002; Moyer et al., 2006; Maher, 2009; Innes et al., 2012). Contrary to these findings, we found no evidence of an association between relatedness and spatial proximity of females in island spotted skunks. Relatedness of female skunks was not negatively correlated with geographic distance, even at the larger spatial scale of combined study sites. Relatedness also was not positively correlated with overlap of home ranges. Hence, our findings join those of the few other studies that have shown a lack of spatial proximity or space sharing by female relatives among solitary mammals (Schenk et al., 1998; Burton and Krebs, 2003; Blundell et al., 2004).

Although increased density often correlates with increased philopatry and kin associations (e.g., Cutrera et al., 2005; Randall et al., 2005), this pattern may break down at very high densities where local competition among kin can promote dispersal (Armitage, 1975; Hamilton, 1996). Further, the competition resulting from high densities might promote increased dispersal distances (Waser, 1985). Thus, unusually high densities in populations and resultant high rates of dispersal out of our study sites could explain why we failed to detect the expected matrilineal structure. Similar results have been noted in other high-density populations of mammals (e.g., Matocq and Lacey, 2004). As proposed by Hamilton (1996), intermediate densities in populations may be best suited for maintaining spatial clusters of kin and promoting kin-based sociality (McEachern et al., 2007).

Alternative explanations for a lack of a matrilineal spatial organization seem unlikely. The male-biased sex ratio in skunks in our study suggests that some adult females may have been present but not studied; however, missing females would affect our results only if the uncaptured females themselves were a biased subset, such as if we consistently failed to capture one female of each dyad of closely-related females. Limited dispersal, a trait sometimes found in mammals on small islands because of the physical constraint of boundaries of the island (Adler and Levins, 1994), might preclude the formation of a gradient of decreasing relatedness with distance. However, Santa Cruz Island is a large island, almost 500 times larger than the typical home range of an island spotted skunk (52 ha; Jones et al., 2008). Limited dispersal also might result if high densities create a social fence that discourages dispersal (Hestbeck, 1982; Matthysen, 2005). However, we did not detect the high levels of relatedness among individuals within study sites that should result from extensive philopatry.

Although we found no evidence of a matrilineal spatial structure, we did find evidence of a patrilineal structure at one study site, Valley Anchorage, where relatedness among males was negatively correlated with distance. The explanation for this pattern is obscure, but it may be related to density, which was about twice as high at Valley Anchorage as at Willows Drainage. Dispersal in spotted skunks has not been studied, but it is possible that density influenced differences in dispersal between sexes, as has been found for kangaroo rats (*Dipodomys spectabilis*; Jones et al., 1988). Hence, perhaps both sexes dispersed beyond the study site at Willows Drainage, but only females did so at Valley Anchorage. Another possibility is that male skunks form coalitions that bring relatives together. Male coalitions have been reported for raccoons (*Procyon lotor*), perhaps in response to a high density of females (Gehrt and Fritzell, 1998).

Our results of spatial organization of the island spotted skunk are consistent with those of other species of solitary mammals, but our findings of no matrilineal spatial structure, along with evidence of a patrilineal structure at one site, are not. Generality of our findings is uncertain because the island spotted skunk is an insular endemic subspecies, and island forms may express differences in density, behavior, and dispersal compared with the mainland (Adler and Levins, 1994). Nonetheless, our study advances our understanding of the spatial and genetic structure of an insular endemic carnivore, the first such study of which we are aware, and perhaps also sheds light on the influence of high densities, at levels rarely achieved on the mainland, on spatial and genetic structure.

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COOPERATIVE BREEDING IN THE GOLDEN-CHEEKED WARBLER (*SETOPHAGA CHRYSOPARIA*)

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ABSTRACT—In May 2009, we observed two male golden-cheeked warblers (*Setophaga chrysoparia*) feeding nestlings at the same nest. We determined the first male was the social mate of the female because we observed him closely following her during construction of the nest and the pair had already made a previous nesting attempt that breeding season. The second male was from a neighboring territory. Our observations demonstrate that cooperative breeding is an alternative mating strategy for this species. We hypothesize that this case of cooperative breeding resulted from an extrapair-copulation between the female and the second male during her fertile period.

RESUMEN—En mayo del 2009, observamos dos machos de *Setophaga chrysoparia* alimentando a los pichones en el mismo nido. Determinamos que el primer macho fue la pareja social de la hembra porque lo observamos siguiendo de cerca a esta hembra durante la construcción del nido y la pareja ya había hecho un intento de poner un nido durante esa temporada de reproducción. El segundo macho fue de un territorio vecino. Nuestras observaciones demuestran que la crianza cooperativa es una estrategia alternativa de apareamiento para esta especie. Suponemos que este caso de crianza cooperativa resultó de una cópula extra-pareja entre la hembra y el segundo macho durante su período fértil.

Avian mating systems in which more than two individuals provide parental care are classified as cooperative breeding systems (Stacey and Koenig, 1990; Emlen, 1991). Examples of parental care include foraging for and feeding young, construction of the nest, incubation, protecting young from predators, and defense of territory (Stacey and Koenig, 1990). This mating system does not appear to be common for birds; only 2.4% (220 of 9,000) of avian species have been characterized as cooperative breeders (Stacey and Koenig, 1990; but see Emlen and Vehrencamp, 1983). Here, we document the first known observation of cooperative breeding behavior for golden-cheeked warblers (*Setophaga chrysoparia*).

This federally endangered Neotropical migratory passerine breeds only in the juniper-oak (*Juniperus ashei*-

Quercus) woodlands of central Texas. Males begin arriving on breeding grounds in early March with females arriving a few days later (Ladd and Gass, 1999). Females begin construction of open-cup nests in mid-March and usually lay three or four eggs per clutch but occasionally five eggs (Pulich, 1976). Males do not assist in construction of nests (but see Lockwood, 1996; Graber et al., 2006), incubation, or brooding but feed females on the nest during incubation as well as nestlings and fledglings. Golden-cheeked warblers begin departing for wintering grounds as early as mid-June although some individuals may remain on the breeding grounds until late August (Ladd and Gass, 1999).

We observed two male golden-cheeked warblers feeding at the same nest in May 2009. We were