



## White-nosed coatis in Arizona: tropical carnivores in a temperate environment

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Intraspecific variation in ranging and social behavior can be perplexing, but also provides an opportunity to assess which behavioral attributes are labile in the face of geographic variation in resources. White-nosed coatis (*Nasua narica*) are group-living carnivores of tropical origin that possess an unusual social system. In the resource-rich tropics, larger-bodied males are solitary, whereas females live in groups (“bands”) along with young of both sexes, but leave them to give birth and wean their young. Males often disperse socially, but not spatially. We studied coatis in the Chiricahua National Monument, Arizona, a resource-poor, arid, and highly seasonal landscape. Using live capture and radiotelemetry in conjunction with microsatellite DNA analyses, we found that Chiricahua coatis exhibited the species-typical pattern of solitary males and gregarious females. Young males left their natal bands as yearlings, and some were found as adults within their natal home range. On the other hand, home ranges were expanded greatly. Bands, and some males, focused their movements in areas several km<sup>2</sup> in extent over periods of weeks or months but shifted those areas markedly among seasons. Some males followed the typical mammalian pattern of natal dispersal beyond their natal area. Rates of movement were higher and female associations appeared to be more flexible than in the tropics. Adult females sometimes ranged singly, not only around the time of parturition, but also when population density was low and occasionally otherwise. In addition, home range overlap was high among both sexes during some seasons, and female bands sometimes fused for prolonged periods. Core patterns of sociality are constant in both resource-rich tropical and resource-poor temperate populations, but coatis appear to make major adjustments in scale of movement and frequency of association in response to resource variation.

Key words: Arizona, coatis, dispersal, group structure, home range, *Nasua*, Procyonidae, social organization

How labile are ranging patterns and social systems in the face of geographic resource variation? This question is fundamental to understanding the evolution of social behavior (Lott 1991). Intraspecific variation and flexibility of social systems has been found in mammals ranging from shrews (Valomy et al. 2015) to primates (Streier 2017) and can provide important insight to critical influences on social systems (Kappeler et al. 2013).

Among carnivores, social structure shows considerable intraspecific variation, complicating reconstruction of its evolutionary history (Dalerum 2007). But that variation also provides the basis for understanding how individual behavioral traits respond to the ecological factors that drive social evolution. For example, intraspecific variation in social structure is most likely explained in terms of local adaptation based on genetic

variation where environments differ strongly among populations, but environmental change is slow (Schradin 2013). Such situations let us explore how individual behavioral tendencies, for example, the propensity to form particular types of social bonds, respond (or fail to respond) to ecological factors. Here, we focus on a group that has radiated into a broad range of ecologically distinctive habitats, the Procyonid carnivores—and in particular the white-nosed coati, *Nasua narica* (hereafter, “coati”).

On Barro Colorado Island, Panama, where they have been studied most extensively, coatis are distinctive in several regards. First, only females are gregarious; males leave bands during their 2nd year and live mostly solitary lives after reaching sexual maturity (Kaufmann 1962; Russell 1981, 1983;

Gompper 1997). Second, males leave their natal bands (“social dispersal”) but they do not usually leave their natal home ranges (“spatial dispersal”—Gompper et al. 1997, 1998). Third, females breed synchronously in their bands but abandon them to give birth, living alone for periods up to a month before and after parturition (Kaufmann 1962; Russell 1982; Gompper 1996).

However, coatis also inhabit tropical dry forest in western Mexico (Valenzuela and Ceballos 2000), and temperate riparian or oak woodland at the northern edge of their range in southeastern Arizona (Ratnayeke et al. 1994; Hass 2002). Among populations, band and home range sizes can differ by an order of magnitude (Gompper 1995), and differences also are reported in patterns of association among males, and between males and female bands (Gompper and Kriansley 1992; Booth-Binczik et al. 2004; Hirsch and Gompper in press). Home range stability may also vary among populations (Hass 2002); in Arizona, even the existence of predictable home ranges has been questioned (Wallmo and Gallizioli 1954; Kaufmann et al. 1976).

Existing studies of procyonid carnivores, particularly coatis and raccoons, provide a variety of hypotheses regarding space use, sociality, and dispersal. Valenzuela and Macdonald (2002) have argued that populations differ in association and space use as predicted from the resource dispersion hypothesis—that band size reflects resource patch richness, but patch dispersion dictates home range size (Macdonald 1983; Johnson et al. 2002). Similarly, Gompper (1996, 1997) has related foraging band size to productivity and food patch size. These hypotheses predict smaller bands and larger home ranges in less-productive areas, and where critical resources (like permanent water) are widely spaced. Similarly, they predict larger home ranges and faster movement during seasonal periods when resources are scarce. Where home ranges (and band sizes) are large, males might be less successful in defending females or resources, leading Booth-Binczik et al. (2004) to suggest that males should then associate more closely with female bands. Gompper et al. (1998) have proposed that the lack of spatial dispersal by males on Barro Colorado Island reflects the importance of resource competition, as opposed to inbreeding avoidance, in driving male emigration. If so, dispersal patterns of males should more closely resemble the mammalian norm in “mainland” populations where dispersal opportunities are less restricted.

Hirsch and Gompper (in press) recently raised another possibility: that phylogenetic inertia constrains the evolution of some aspects of coati sociality, in particular the social isolation of males. At the same time, they emphasized that the broad range of habitats used by coatis creates an opportunity to study the degree of population-level plasticity. Studies of intraspecific behavioral variation in other mammalian taxa are rapidly expanding (Maher and Burger 2011; Kappeler et al. 2013; Schradin 2013), but which traits tend to respond to local ecological conditions, and which are constrained?

Here, we address this question for procyonid carnivores, using data on coati movements and associations from a radio-tracking study spanning 9 years in the open forests of the

Chiricahua Mountains in southeastern Arizona. In Arizona, the climate is arid and seasonal, productivity is low, and coatis are at the extreme northern edge of their geographic range (Kaufmann et al. 1976; Lanning 1976). We ask, do coatis in this environment exhibit the patterns of ranging, band cohesion, and dispersal described for tropical coati populations, as expected from what we consider the null hypothesis of phylogenetic inertia? We examine sex and seasonal variation in rates of movement; home range size, stability, and overlap; social cohesion among males and females; and dispersal. Where the data suggest intraspecific variation, we ask which ecological hypotheses best predict the observed results. But more generally, we ask which behavioral traits are labile in the face of ecological variation, and which are not?

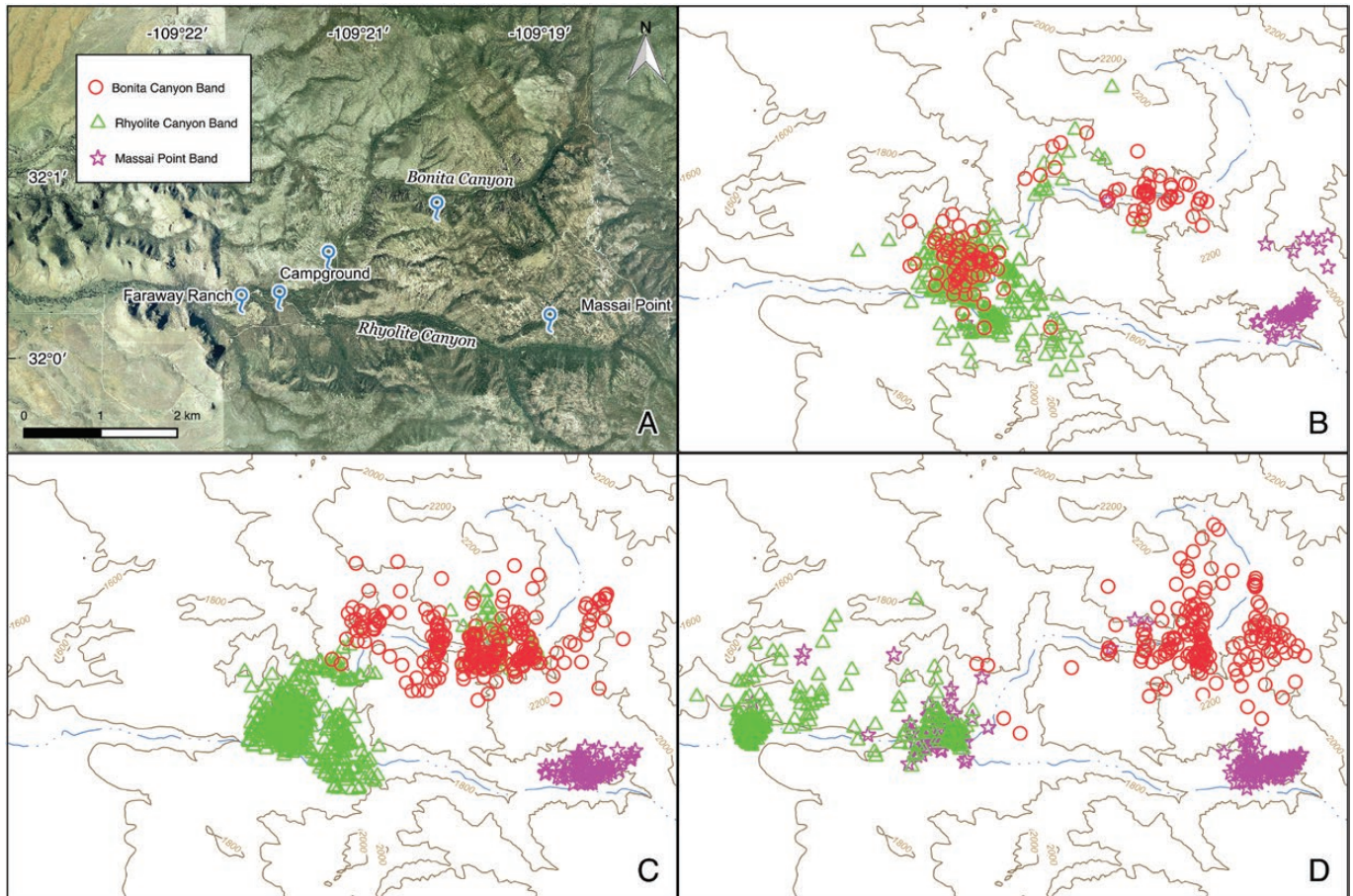
## MATERIALS AND METHODS

*Study site.*—Chiricahua National Monument (31°60.5'N, 109°19.0'W, hereafter CNM) is a ~50-km<sup>2</sup> preserve within the Chiricahua Mountains of southeastern Arizona, a high-elevation “sky island” (1,580–2,200 m) isolated by surrounding deserts. The climate is highly seasonal, with winter low temperatures frequently < 0°C and June highs > 30°C. Annual rainfall during this study ranged from 20 to 60 cm, with most rain during the July–September “monsoon” season and, less reliably, between December and February. Rainfall patterns ensure that the mainstays of CNM coati diet (litter invertebrates, reptiles, seeds, and fruits) are most available in late summer and fall, declining in availability during the winter and spring (Ballinger 1979; Koprowski and Corse 2001).

Topography is rugged, with steep-walled canyons channeling seasonal streams. During much of the year, water is confined to small rock pools and permanent springs. Canyon bottoms contain riparian woodland, within which the fruits of junipers (*Juniperus* spp.), oaks (*Quercus* spp.), and madrone (*Arbutus arizonica*) are key food sources for coatis. Away from canyon bottoms, important coati food sources include manzanita (*Arctostaphylos pungens*), prickly pear (*Opuntia*), yucca (*Yucca schottii*), agave (*Agave* spp.), and a diversity of invertebrates, lizards, and snakes (Kaufmann et al. 1976; McColgin et al. 2003). We did not attempt to quantify food distribution, but did map sources of permanent water (Fig. 1A). Potential predators of adult or juvenile coatis in CNM include pumas (*Puma concolor*), black bears (*Ursus americanus*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and large raptors (including *Aquila chrysaetos*, *Strix occidentalis*, and *Buteo* spp.—Kaufmann et al. 1976; Hass and Valenzuela 2002).

We trapped and followed CNM coatis between 1996 and 2004. We radiotracked coatis during periods of 1–2 months during winter (December–February 1998–1999, 2003–2004), spring (March–May 1999, 2001–2004), summer (June–August 1996–1998), and fall (September–November 1998). In CNM, coatis breed during late March and early April, and give birth in July (Kaufmann et al. 1976). Animal trapping and handling procedures conformed to guidelines of the American Society of Mammalogists (Sikes et al. 2016) and were approved by





**Fig. 1.**—Home ranges of 3 Chiricahua National Monument (CNM) coati (*Nasua narica*) bands, 2002–2004. A) Aerial view of the CNM study site, Arizona, September 2004 (image: Google Earth, Digitalglobe) showing the distribution of riparian woodland and the location of the 5 permanent sources of water. Note that coatis used all parts of Rhyolite Canyon, but could not be radiolocated in its central section because steep canyon walls prevented reliable triangulation there. B)–D) Triangulated radiolocations of adult females in the Bonita Canyon, Rhyolite Canyon, and Massai Point bands during spring 2002 (511 locations), 2003 (901 locations), and 2004 (657 locations), respectively. Contour interval = 200 m.

Arizona Game and Fish, the National Park Service, and the Purdue University IACUC.

**Capture.**—Coatis were captured using live traps measuring  $102 \times 35 \times 35$  cm (Tomahawk Live Traps, Tomahawk, Wisconsin), baited with wet cat food. Traps were set in the morning, checked twice per day, and closed in the evening. We flushed captured individuals from the live trap into a handling cone (Koprowski 2002). Age was determined from body size (adult > 2 years, yearling = 1–2 years, juvenile < 1 year). Sex was determined, and individuals were weighed (to the nearest 0.1 kg), checked for reproductive condition, and given Monel ear tags (National Band and Tag, Newport, Kentucky). We duct-taped unique color bands on the tip of adults' tails, and fitted them with radiocollars (115–130 g, 2-year battery life; Wildlife Materials, Carbondale, Illinois). We took a tissue sample from each individual's ear using standard hog ear-notchers. Visual sightings suggested that > 85% of adult females in bands were marked.

**Radiotracking.**—Thick vegetation, rugged terrain, and low numbers of coatis in CNM made it rare to actually see them. We therefore examined coati movement and association patterns during daylight hours, using trap records and locations

triangulated from fixed locations once per hour (1996–1999) or 2 h (2001–2004). If we ascertained compass bearings for a given individual from  $\geq 2$  fixed locations within 30 min, we estimated its UTM coordinates using program Locate II (<http://www.nsac.ns.ca/envsci/staff/vnams/locate.htm>).

Because we could rarely confirm coati locations visually due to complex topography and the scale of coati movements, we took several steps to purge our data set of dubious radiolocations. First, given the bearing errors we estimated using fixed transmitters, we distrusted fixes from bearings that differed by  $< 45^\circ$  or  $> 135^\circ$ . Second, we were skeptical of any locations that suggested coati movements exceeding 2 km/h. Finally, we analyzed “viewsheds” (<https://caltopo.com/>) to ascertain what parts of CNM were visible from our fixed triangulation points. Some signals, presumably because of reflection, were triangulated to points behind cliffs or hills. We removed all such points from our data set.

**Rates of movement.**—We estimated speed by dividing the distance that an individual moved since its previous radiolocation by the number of hours transpired, using only points separated by  $\leq 2$  h.

**Home range size, stability, and overlap.**—We used program R (with code from J. Fieberg adapted by R. Swihart) to determine

home range sizes (Fieberg 2014; R Core Team 2015). We estimated seasonal home ranges for the subset of radiocollared individuals for which we had > 30 locations, and long-term home ranges for those with > 50 locations during the course of the study, using locations separated by  $\geq 4$  h to reduce problems related to spatial autocorrelation (Otis and White 1999; Seaman et al. 1999).

We report 95% utilization distribution kernel density values using direct plug-in bandwidth estimation. For comparison with other studies, we calculated the home range overlap between individuals A and B as the percentage of A's 95% utilization distribution overlapped by B, averaged with the percentage of B's home range overlapped by A (Fieberg and Kochanny 2005). As a measure of an individual's (or a band's) home range stability, we report overlaps between its home range during the 1st season sampled and its subsequent seasonal home ranges (Hass 2002; Edwards et al. 2009).

*Social cohesion.*—We defined social groups by examining the spatial separation within dyads of individuals that were located “simultaneously” (< 30 min of each other). Preliminary analysis indicated surprisingly large estimated distances between adult females and their nearest adult female neighbors (median = 260 m). Individuals more than 100 m apart are likely out of visual and acoustic contact with one another, but our estimates of nearest neighbor separation are biased upwards by triangulation error and by the fact that individuals may travel substantial distances during the 30-min interval we defined as “simultaneous.”

We calculated the mean separation between the members of every female dyad on every day for which simultaneous tracking data were available. The distribution of female–female separation distances was bimodal, with a sharp drop-off around 500 m and a secondary peak above 1,000 m. We were again surprised to find that, for a given dyad, this distance could vary widely both seasonally and from day to day. During each season, we assigned females to the same band if > 33% of their daily separation distances were < 500 m. Conversely, if 2 females were > 1,000 m apart in > 33% of their samples, we considered them to be members of different bands. We used dyadic distances to explore seasonal variation in female band cohesion and the possibility of associations involving adult males. We did not radiotrack juveniles and yearlings, but assigned them to a band if we trapped them < 250 m from other band members.

To explore interaction patterns of putative band members in more detail, we performed a variation of Doncaster's (1990) dynamic interaction analysis, in effect a randomization test (cf. Gehrt and Fritzell 1998a). For each dyad, we drew a location randomly from the set of observed locations for one member, along with a random location used by the other dyad member on a different day. We calculated the distance between these 2 locations and iterated this process 1,000 times. This procedure creates the distribution of separation distances expected if each individual is moving independently within its home range, without regard to the presence or absence of the 2nd individual. Comparing these separation distances with those actually observed indicates whether the 2 individuals are attracted

to, repelled by, or ignore each other. We used  $\alpha = 0.05$ ; for example, if members of a dyad were located within 500 m of each other more often in reality than they were in 95% of our random simulations, we considered this evidence of attraction.

*Microsatellite genotyping.*—We used genotypes to identify recaptured individuals that had lost ear tags and to infer young animals' natal bands. Tissue samples were transported to Purdue University in a saturated solution of DMSO and NaCl, removed from solution, and stored at  $-80^{\circ}\text{C}$ . DNA was extracted using a DNeasy tissue kit (Qiagen Sciences Inc., Germantown, Maryland) and PCR was used to amplify DNA using microsatellite primers originally developed for kinkajou (*Potos flavus*), black bears (*U. americanus*), and American martens (*Martes americana*)—Kays et al. 2000; Booth-Binczik 2001).

Coatis showed variation at 8 loci (2–8 alleles per locus—McColgin 2006). Of these, 1 (*Pfl4*) showed signs of null alleles, so our assignments are based on the remaining 7 loci. PCR mix for all primers contained: 1  $\mu\text{l}$  template DNA, 1.1  $\mu\text{l}$  DNTPs, 0.12  $\mu\text{l}$  forward primer, 0.12  $\mu\text{l}$  reverse primer, 1.2  $\mu\text{l}$  MgCl<sub>2</sub>, 1.5  $\mu\text{l}$  buffer, 1.2  $\mu\text{l}$  BSA, 0.2  $\mu\text{l}$  Taq polymerase, and 8.56  $\mu\text{l}$  deionized H<sub>2</sub>O. Cycling for primers *Pfl2*, *Pfl3*, *Pfl9*, *Pfl11*, and *Ma3* was as follows: 5 min at  $94^{\circ}\text{C}$ ; 30 cycles of 45 s at  $94^{\circ}\text{C}$ , 45 s at annealing temperature, 60 s at  $72^{\circ}\text{C}$ ; then 30 min at  $72^{\circ}\text{C}$ , and hold at  $4^{\circ}\text{C}$ . Cycling for primers *Pfl4*, *G10H*, and *Ma9* was as follows: 1 min at  $94^{\circ}\text{C}$ ; 4 cycles of 30 s at  $94^{\circ}\text{C}$ , 20 s at annealing temperature, 5 s at  $72^{\circ}\text{C}$ ; followed by 34 cycles of 15 s at  $94^{\circ}\text{C}$ , 20 s at annealing temperature, 1 s at  $72^{\circ}\text{C}$ ; then 30 s at  $72^{\circ}\text{C}$ , and hold at  $4^{\circ}\text{C}$ . PCR products were diluted, run on polyacrylamide gels on an ABI 377 DNA sequencer, and analyzed using GeneScan Analysis 3.1 and Genotyper 2.0 (Applied Biosystems, Foster City, California).

*Dispersal.*—We defined a yearling as leaving its natal band (“social dispersal”) if we trapped it > 500 m from that band. Radiotracked adults were considered to have dispersed socially if we consistently located them > 500 m from all radiotracked members of their natal band. We examined “spatial” dispersal by comparing the mean UTM coordinates of an individual's natal band's home range during the season in which it was born with the mean of coordinates at which it was located as a yearling or adult.

We attempted to assign a natal band for each juvenile and yearling from its microsatellite genotype, using CERVUS 3.0.7 (Kalinowski et al. 2007). We first narrowed the candidate parent pool by examining trapping records. If an adult female was captured during the inferred birth year of the offspring, or in the year preceding it, we considered it as a possible parent. CERVUS assigned mothers (and thus natal bands) to 6 young coatis at 95% certainty. In 4 additional cases, CERVUS failed to assign a mother with > 95% certainty because there were  $\geq 2$  candidates with no allelic mismatches and high log odds (LOD) scores. In each case, those females were members of the same band, so that we could use LOD scores to infer a natal band with 95% confidence. In these 10 cases, the young animal was still associated with its genetically inferred band when first captured. As a result, we felt confident in assuming that 9 additional juveniles trapped with adult females (but without a CERVUS-assigned mother) were still with their natal bands.



**Statistics.**—Seasonal and sex differences in body mass, home range size, speed, and nearest neighbor distance were analyzed with SAS version 9.4 (SAS Institute Inc. 2013). Analyses included data from all years, but sample sizes from fall were adequate only for analyses of speed. We used PROC MIXED with autoregressive covariance structure to account for the fact that individuals were sampled repeatedly. Season and sex were fixed effects and we set  $\alpha = 0.05$ . Where necessary, we log-transformed the data to ensure normality; to visualize sex and seasonal patterns, we report medians and ranges. We initially tested models including interactions, but when they were not significant, we reran the model without them.

## RESULTS

We marked a total of 55 adult coatis (34 female, 21 male), 28 yearlings (10 female, 18 male), and 14 juveniles (4 female, 10 male). Estimated population density declined over the study from a peak of 0.5 adults/km<sup>2</sup> in 1998 to a low of 0.1 adults/km<sup>2</sup> in 2004. Annual disappearance rates from the study population were 0.3 for adult females (13 disappearances in 48 animal-years, excluding observations that were censored because we lacked data from 2000 and 2005) and 0.4 for adult males (11 disappearances in 29 animal-years). Young animals disappeared at higher annual rates: 0.8 for yearlings (7/9 females, 10/12 males) and 0.6 for juveniles (0/3 females, 5/6 males). No adult was observed alive for more than 4 years.

Adult females (median 3.8 kg, range 2.9–5.2 kg) were lighter than adult males (median 5.0 kg, range 3.4–7.7 kg). Body mass was greatest in winter, declining from winter through spring to summer for females (winter: median 4.0 kg, range 2.9–5.0 kg; summer: median 3.2 kg, range 2.8–3.8 kg) and especially for males (winter: median 5.9 kg, range 4.6–7.7 kg; summer: median 4.3 kg, range 3.4–5.3 kg). Effects of sex ( $F_{1,49} = 57.15$ ,  $P < 0.0001$ ), season ( $F_{2,23} = 54.04$ ,  $P < 0.0001$ ), and their interaction ( $F_{2,23} = 11.73$ ,  $P = 0.0003$ ) were all significant.

During years of low population density (2001–2004), we were aware of 3 female bands, with home ranges initially centered in Rhyolite Canyon, in Bonita Canyon, and near Massai Point (Fig. 1). These bands were small, containing 2–6 adult females in 2002 but only 1–2 adult females (each with associated juveniles and yearlings) by 2004. All known adult females were unambiguously members of one of these bands. During years of high density (1996–1999), band membership was less easily defined. During this period too, we were aware of 3 bands, but these bands were larger (3–9 adult females plus associated young) and as we note below, membership was less stable.

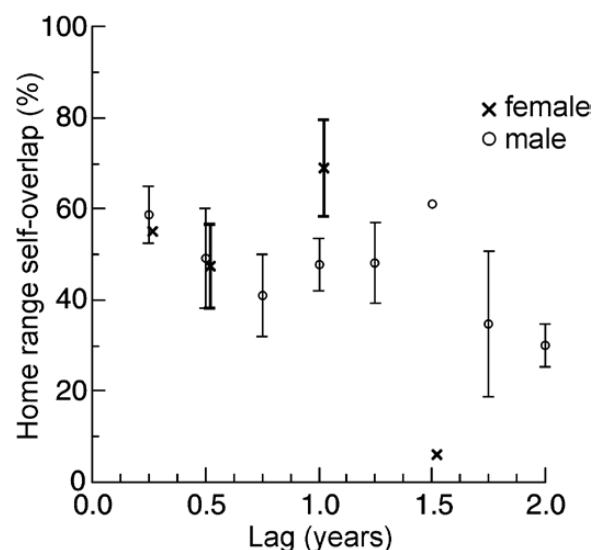
**Rates of movement.**—Males moved faster than females (females: median 182 m/h, range 0–1,550 m/h; males: median 210 m/h, range 10–1,790 m/h;  $F_{1,48} = 5.92$ ,  $P = 0.02$ ) and both sexes traveled at different speeds across seasons. Speeds were highest in summer (winter: median 179 m/h, range 10–950 m/h; spring: median 158 m/h, range 0–1,400 m/h; summer: median 257 m/h, range 10–1,790 m/h; fall: median 204 m/h, range 0–1,320 m/h;  $F_{3,52} = 31.30$ ,  $P < 0.0001$ ). Because coatis did not

move in straight lines between telemetry fixes, these values of speed are actually underestimates.

**Home range size.**—Annual home ranges were large and 95% kernel estimates did not differ between the sexes (medians: female 4.6 km<sup>2</sup>, range 2.2–7.5 km<sup>2</sup>; male 4.6 km<sup>2</sup>, range 1.5–11.6 km<sup>2</sup>,  $F_{1,37} = 0.64$ ,  $P = 0.43$ ). Home range size estimates for female bands (median 4.6 km<sup>2</sup>, range 3.3–7.7 km<sup>2</sup>) were comparable to those for individual females. These estimates are lower limits of true home range size, because we did not track coatis throughout the year, and because some parts of CNM were not visible from our triangulation points.

Although annual home ranges were large, during any given season coatis concentrated their activities in smaller areas. We detected no differences in seasonal home range size between the sexes (females: median 3.0 km<sup>2</sup>, range 0.9–9.5 km<sup>2</sup>; males: median 2.9 km<sup>2</sup>, range 0.3–9.9 km<sup>2</sup>;  $F_{1,21} = 0.27$ ,  $P = 0.61$ ) but the areas used were much larger in summer than in winter or spring (winter: median 1.4 km<sup>2</sup>, range 0.3–9.5 km<sup>2</sup>; spring: 2.9 km<sup>2</sup>, range 0.9–9.9 km<sup>2</sup>; summer: median 4.7 km<sup>2</sup>, range 1.9–6.3 km<sup>2</sup>;  $F_{2,10} = 16.31$ ,  $P = 0.0007$ ).

**Home range stability.**—Both males and females moved substantially between seasons; about one-half the area used by an individual in any given season had not been used in the previous season. Over the longer term, range use was more stable (Fig. 2). If coatis had been nomadic, home ranges sampled in different seasons would have overlapped less and less as the lag between the sampled seasons increased (Hass 2002). We detected no such trend ( $F_{7,23} = 1.45$ ,  $P = 0.23$ ), and patterns shown by individual males and female bands did not differ ( $F_{1,22} = 0.26$ ,  $P = 0.64$ ). Both males and females shifted their



**Fig. 2.**—Home range stability for adult coatis (*Nasua narica*) in Chiricahua National Monument, Arizona, as indicated by the percentage of a male individual's or female band's seasonal home range that was overlapped by that same individual's or band's home range up to 2 years later. Data are mean  $\pm$  SE for 3 female bands and 6 males that were tracked for  $\geq 1$  year between 1996–1999 and 2001–2004. On this graph, home range drift would show up as a pattern of decreasing self-overlap as “lag” increases.

home ranges from one season to the next, but each individual (or band) shuttled among a limited set of areas.

Although home ranges were generally stable over the long term and all coatis shifted the areas used from season to season, a few individuals showed more complex patterns of home range use. Of 10 adult males radiotracked for > 1 year, 6 had home ranges that changed little (Fig. 3A). Others, however, shifted their centers of activity by several km from one season to the next (Fig. 3B).

As with males, we found considerable variation among adult females in home range stability. Most females tended to shift among a limited set of seasonal home ranges, and across years, the same areas were revisited repeatedly. The only unambiguous case of home range drift by adult females occurred in 2003–2004, during a dramatic population decline. The Bonita Canyon band, which had used a relatively well-defined area during 2002 and 2003 (Figs. 1B and 1C), moved about 2 km down-canyon in 2004 to the vicinity of Faraway Ranch, an area not previously used by any radiotagged animals (Fig. 1D).

**Home range overlap.**—Over the long term (the lifetime of our radios), home range overlap was high; 95% kernel overlap was as high as 73% among males and 86% among female bands. Seasonally, home range overlap varied enormously in both sexes. During some seasons (summer 1997, spring 2002), we detected no male–male home range overlap at all; in other seasons (most notably winter 1998) male dyads overlapped as much as 82%. Similarly, between pairs of female bands seasonal overlap varied from 0% to 80%. High seasonal overlap seemed more common during years of high density, and more common in winter than later in the year, but our samples were inadequate for statistical analysis.

**Social cohesion: males.**—Adult males showed no signs of gregariousness. The median distance between an adult male and his nearest male neighbor was 833 m (range 30–5,670 m). Male–male nearest neighbor distances were shortest in winter (winter: median 357 m, range 40–5,670 m; spring: median 812

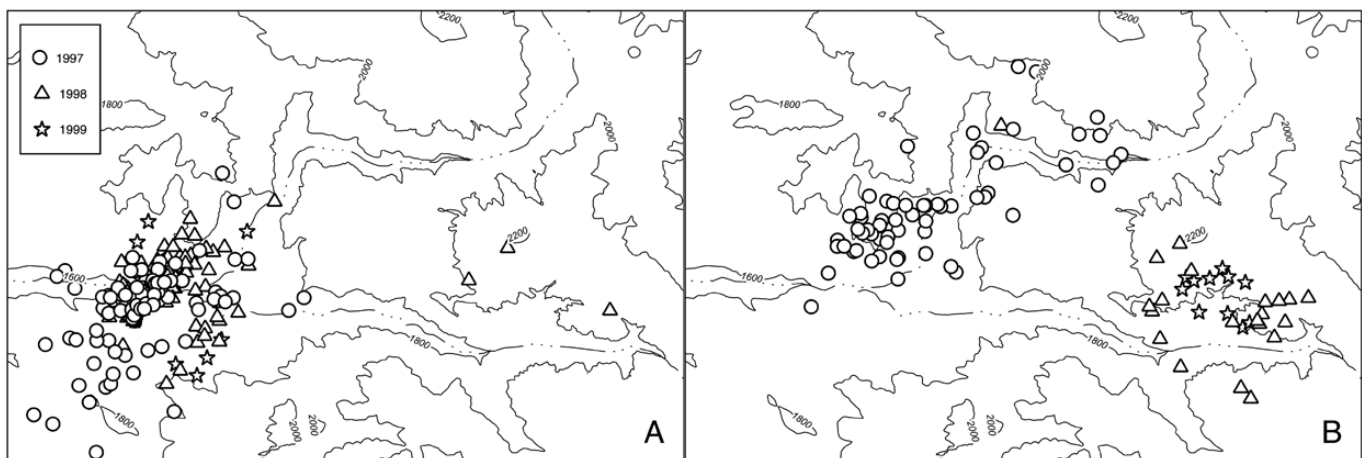
m, range 30–4,630 m; summer: median 977 m, range 80–5,380 m;  $F_{2,15} = 11.14$ ,  $P = 0.001$ ).

Most males clearly led solitary lives, but a few male–male dyads exhibited substantial seasonal home range overlap. We found 10 male dyads with separation distances averaging < 500 m and sample sizes adequate to test for attraction or avoidance using our dynamic interaction analysis. Nine of these cases were in winter 1998, when coati density was particularly high, and none lasted for > 1 season. Among these dyads, we detected no sign of mutual avoidance, and in 6 of 9 cases males were located < 500 m from each other significantly more often than expected from the null hypothesis of independent movement.

**Social cohesion: females.**—Nearest neighbor distances among females, while substantial (median 260 m, range 10–6,360 m), averaged less than one-third of those for males. Female bandmates were even closer together (median 249 m, range 10–3,960 m). Females were separated from their nearest bandmates by much greater distances in the summer (median 385 m, range = 20–3,960 m) than during the winter (median 222 m, range 20–2,210 m) or spring (median 232 m, range 10–1,490 m;  $F_{2,30} = 24.62$ ,  $P < 0.0001$ ).

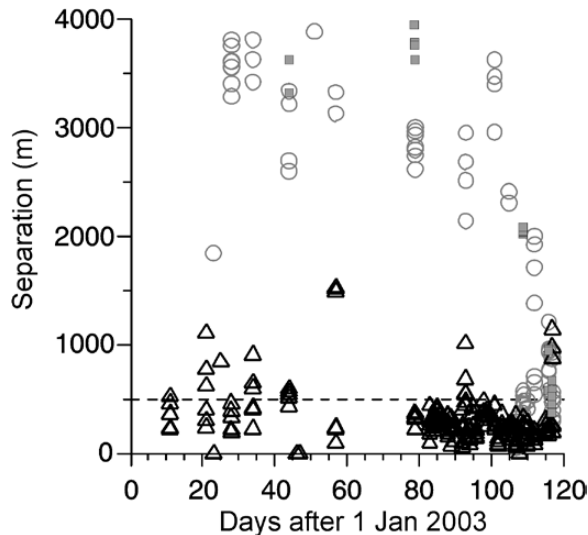
Social cohesion among females also was variable in other ways. During high-density years, large day-to-day variation in nearest neighbor distances suggested that bands sometimes fissioned into smaller subgroups for periods of a day or more. In addition, during winter samples in 1997, 1998, 1999, and 2004, bands coalesced. During periods of apparent band fusion, members of different bands mingled, and dyadic distances were comparable between females in the same or different bands. Band fusion occurred most often during the winter, but not always. During 2002 and 2003, the 3 bands were widely separated during our winter samples, but in 2003 they then coalesced during April (Fig. 4).

Dynamic interaction analyses confirmed that female bandmates were attracted to each other. We had simultaneous radiotracking data for 81 female dyads that fulfilled our definition of bandmates. In all 81 dyads, the proportion of time females



**Fig. 3.**—Home ranges of 2 adult male coatis (*Nasua narica*) in Chiricahua National Monument, Arizona, radiotracked from summer 1997 through spring 1999. Location and scale are the same as in Fig. 1. A) Male 120 used essentially the same home range throughout this 2-year period (270 locations). B) Illustrating a less stable pattern, male 216 dramatically shifted his seasonal home range toward the E midway through 1998 (146 locations).

spent < 500 m apart was significantly greater than expected from the null hypothesis of independent movement. During periods of group fusion, dynamic interaction analysis confirmed attraction between females in different bands, as well as between bandmates.



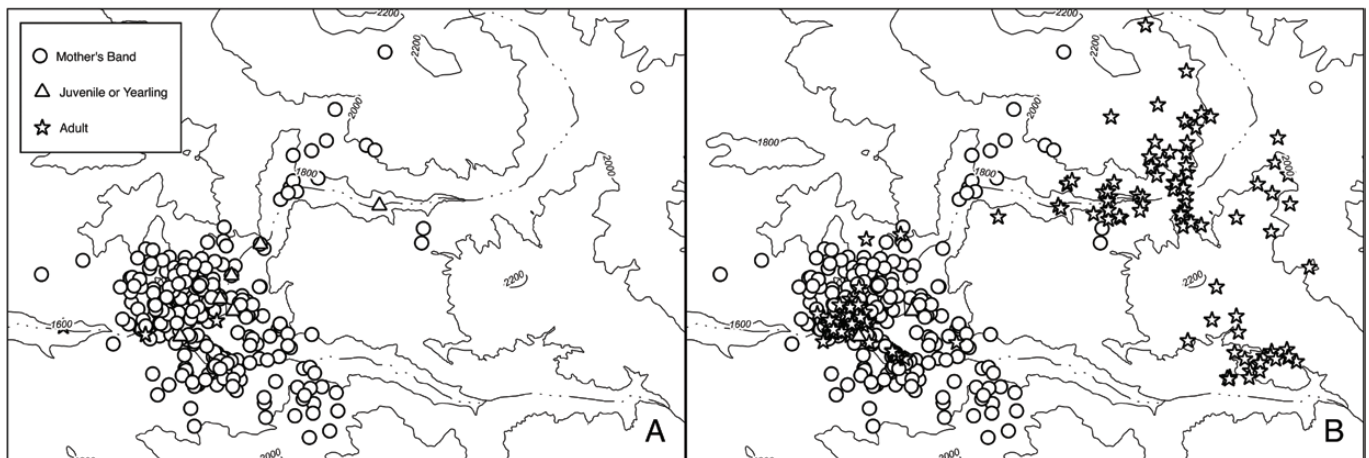
**Fig. 4.**—Separation between adult female coatis (*Nasua narica*) in the Bonita Canyon band, Chiricahua National Monument, Arizona, and other adult females in their own and different bands during 2003 ( $n = 320$ ). During January and February (days 20–60), Bonita Canyon females were nearly always separated by at least 3 km from females in the Rhyolite Canyon (squares) and Massai Point (circles) bands. Females belonging to the Bonita Canyon band were generally located < 500 m (dashed line) from their bandmates (triangles); exceptions indicate occasional subgroup formation. During March and April (days 60–120), members of all 3 bands drifted together and the bands fused near the end of April.

During late 1998, the Rhyolite Canyon band apparently disintegrated. Six adult females were associated with this band during 1998, but by the beginning of 1999, 3 had disappeared and 1 had transferred to the Bonita Canyon band. The remaining 2 adult females were tracked into spring 1999 as independent solitaires. During this period, each was > 500 m from any other simultaneously located female > 95% of the time.

**Female–male association.**—The distances between adult females and their nearest adult male neighbors (median 616 m, range 10–5,610 m) were intermediate between female–female and male–male nearest neighbor distances. Although we occasionally triangulated males and females to locations within 100 m of each other, no such associations lasted for > 1 day. Even during the spring breeding season, dynamic interaction analysis detected no cases of significant female–male attraction. Female–male distances were shorter during winter (median 465 m, range 20–3,610 m) than during spring (median 684 m, range 10–5,150 m) and summer (median 658 m, range 20–4,620 m;  $F_{2,29} = 13.9$ ,  $P < 0.0001$ ).

**Social dispersal.**—The majority (12 of 19) of males that we trapped as yearlings were alone when they were trapped. In contrast, 12 of 13 females trapped as yearlings were in a band. Five females and 5 males with known natal bands were trapped or tracked as yearlings or adults. Four of the 5 males had either moved to another band or were alone. In contrast, 4 of 5 females were still in their natal bands.

**Spatial dispersal.**—The fact that yearlings disappeared at higher annual rates than juveniles suggests that some yearlings dispersed off-site. We knew distances between seasonal home range centers of yearlings or adults and those of their natal bands for 5 males (median 1,860 m, range 350–3,870 m) and 5 females (median 850 m, range 720–1,690 m). Like all 5 females (Fig. 5A), 2 of 5 males continued to range within the area used by their natal band, but 3 moved outside it,



**Fig. 5.**—Natal dispersal by 2 coatis (*Nasua narica*) in Chiricahua National Monument, Arizona, with known natal groups. Location and scale are the same as in Fig. 1. A) Female 272 was born in 2001 and genetically assigned to a mother in the Bonita Canyon band. She was captured with her mother's band as a juvenile in 2002, as a yearling in 2003, and then as an adult in spring 2004 (356 locations). B) Male 601, also born in the Bonita Canyon band in 2001, remained within that band's range through his yearling year. By the beginning of his 1st year as an adult, he had dispersed socially and during that spring he moved E, where he was subsequently radiotracked alone in an area outside that used by his natal band (482 locations).



including the individual with the most extensive radiotracking data (Fig. 5B).

## DISCUSSION

*Ranging patterns.*—Low annual rainfall, long dry seasons, and cold winters in CNM limit productivity there. Consistent with this fact, CNM coatis live at the lowest densities reported for any *Nasua* population, as low as 0.1/km<sup>2</sup>. This density is 2 orders of magnitude lower than that attained by coatis in Central American forests (Kaufmann 1962; Gompper 1997; Booth-Binczik 2001).

Home ranges of many carnivores, including coatis and other procyonids, tend to increase with increasing latitude, presumably reflecting trends in productivity (Gompper and Gittleman 1991; Valenzuela and Ceballos 2000; Prange et al. 2004). Consistent with this pattern, CNM coatis (both male and female) use home ranges at least an order of magnitude larger than those reported for coatis in Panama (Kaufmann 1962; Russell 1982), and comparable in size to those reported in more southerly Arizona populations (Ratnayeke et al. 1994; Hass 2002).

In wet tropical habitats, the rainy season is a period of peak food production for coatis (Gompper 1995). This is not true, however, in southern Arizona. Whereas seasonal monsoon rains in CNM generally begin in July, watercourses do not run reliably until August, and the fruits or seeds of oaks, juniper, manzanita, and other species important to coatis do not mature until late in the year. Thus, food sources are scarce during the spring and early summer (Valenzuela and Ceballos 2000; CNM coati body masses are lowest in those seasons), and water sources become widely scattered then. If CNM coatis adjust their ranging to seasonal resource variation, home range size should increase from winter into spring and summer. We found this predicted pattern in both sexes.

Like home range size, aspects of movement within the home range were impacted by CNM's low productivity and seasonality. While foraging, CNM females move approximately 25% faster than those in Panama (Kaufmann 1962) and at speeds similar to those reported in Mexican dry forest (Valenzuela and Ceballos 2002). Speeds are higher in the less productive dry season, and are higher for males, the larger sex, than for females.

The large scale of CNM coati movements makes it easy to see how early studies (Wallmo and Gallizioli 1954) concluded that Arizona coatis might be nomadic. Kaufmann et al.'s (1976:624) characterization that "bands appear in one canyon complex, are conspicuous residents for weeks and months and then disappear" remains appropriate and consistent with the impressions of many local residents on both sides of the Chiricahuas. Our data support the conclusions of Hass (2002), studying coatis elsewhere in Arizona, that home ranges are stable across years. Hass reported that bands used large areas but, over the long term, showed a tendency to shift core areas within them in a circular pattern. In our study, home range centers could shift several km from one season to the next, but with 1 exception

these shifts occurred within a circumscribed area and the individuals were likely to return, a few months or a year later, to the same canyon.

*Dispersal.*—Like males in most mammals, CNM males dispersed socially, leaving their natal groups as yearlings, whereas females generally did not. Natal dispersal by females is rare among coatis (but see Gompper et al. 1997), and we found only 1 possible case.

Our observations of spatial dispersal suggest the possibility of wider movements by males than has been reported from Panama. There, both the spatial distribution of genetic similarity and data from radiotracking indicate that most adult males inhabit an area within or overlapping their natal home range (Gompper 1997; Gompper et al. 1998). Few data exist on spatial dispersal in other populations. Hass (2002) tracked 1 male to adulthood on a home range that overlapped that of its natal group by ~50%. In contrast, the majority of CNM males dispersed over distances up to 4 km, and the individual for which our data are most extensive settled adjacent to, but outside the range of his natal band (Fig. 5B). In addition, long-distance dispersal may have contributed to the high rate at which yearlings disappeared. Kaufmann et al. (1976) reported sighting a male with distinctively torn ears that, if the damage was done by ripped-out ear tags, had dispersed > 20 km from CNM.

*Social cohesion: males.*—Although previous studies have occasionally reported adult male coatis associating with female bands outside the breeding season (Wallmo and Gallizioli 1954; Gompper and Kriansley 1992; Booth-Binczik et al. 2004), males are nearly always encountered alone, and females' reactions to males are usually aggressive (Gompper 1996). In CNM, neither dyadic distances nor dynamic interaction analyses suggested any tendency for males to associate with bands over periods longer than a day. Moreover, adult males were nearly always widely separated from each other. The few possible exceptions (indicated by dynamic interaction analysis) occurred at high population density, and even in these cases, males did not travel within sight of each other.

*Social cohesion: females.*—Adult female coatis in Panama and Guatemala live in closely associating matrilineal groups (Kaufmann 1962; Booth-Binczik et al. 2004). Based on patterns of natal dispersal, nearest neighbor distances, and dynamic interaction analyses (and also on estimates of genetic relatedness—McColgin 2006), matrilineal structure also characterizes CNM bands, but in Arizona, band structure appears looser and more flexible than that reported from tropical populations.

Band structure was particularly nebulous during 1996–1999, when coatis were more numerous. Close association among females from different bands was common during these years, and different bands used highly overlapping home ranges. Temporary band fusion in other coati populations has generally been associated with large, productive food patches (Kaufmann 1962; Russell 1983). In CNM, band fusion is more likely related to the distribution of limited sources of water, as it is most common during winter and spring when seasonal streams dry up. Perhaps the common thread is increased tolerance in the presence of patchy and shareable resources; home ranges of



adult males also converge and male–male home range overlap increases during periods of band fusion.

When CNM bands were not fused, bandmates could be widely separated. During the summer, nearest neighbor distances doubled when pregnant females left, gave birth, and weaned their offspring. Some females were regularly located > 3 km from other members of their band. Band disassociation around the time of parturition appears to be universal among coatis (Kaufmann 1962; Ratnayeke et al. 1994), but CNM bands also appeared to fragment for periods of hours or days during other seasons. Coati bands have been observed to split into temporary foraging subgroups in Panama; smaller subgroups were found when resources were scarcer (Russell 1983; Gompper 1997). Subgroups among CNM females likely reflect a similar phenomenon. Also during high-density years, some adult females spent substantial periods outside any group, in 1 case transferring between bands and in others foraging in isolation for periods of months. Immigration by adult females into bands has also been observed in other populations, sometimes (as in CNM) associated with band disintegration (Russell 1983; Gompper 1997; Hass 2002).

The numbers of adult females per band in CNM (1–9) are at the low end of those reported from tropical populations (2–24—Gompper 1995; Booth-Binczik 2001), as posited by the resource dispersion hypothesis (Johnson et al. 2002). Band size declined during our study as a result of high mortality and poor recruitment (the number of bands remained constant). The decline may reflect unusually low annual rainfall during later years of the study (mean 26 cm during 2000–2003). Band size also was small and declining in Hass' (2002) population, ~100 km from CNM and subject to similar rainfall trends. An alternative possibility is that coati numbers and band sizes decreased due to disease. Several rabid foxes were encountered in CNM during 2002–2004, and other coati population crashes both there and elsewhere were caused by rabies, canine distemper, or mange (Kaufmann et al. 1976; Valenzuela et al. 2000; Funk et al. 2001).

*Phylogenetic inertia.*—Comparing CNM and other coati populations suggests that ranging behavior is little constrained by phylogenetic inertia. The scale and pattern of daily and seasonal movement are labile not only among coatis, but also among other procyonids for which data are adequate (ring-tailed coatis, *Nasua nasua*—Beisiegel and Mantovani 2006; Costa et al. 2009; Hirsch and Gompper in press; raccoons, *Procyon lotor*—Gehrt and Fritzell 1998a; Prange et al. 2004; Schuttler et al. 2015). In coatis as well as in other procyonids, cross-population trends in speed of movement, seasonal home range size, and seasonal home range overlap are consistent with qualitative trends in habitat productivity and resource dispersion (Johnson et al. 2002; Valenzuela and Macdonald 2002).

Whereas ranging patterns and band sizes vary widely within and among procyonids, other attributes of sociality are more constrained by phylogeny. For example, female bands also fragment around the time of parturition in the ring-tailed coati (Beisiegel and Mantovani 2006). In understanding the evolution

of procyonid social structure, it might be fruitful to distinguish *Nasua* as a genus whose females are solitary when pregnant and lactating, but tend to join other females (especially related ones) during other parts of the year.

In all coati populations for which data exist, females are philopatric and tolerate their own daughters into adulthood. In CNM, dispersal by females is rare and female affiliation with adult daughters persists even at extremely low population density. Female philopatry also is the norm in the ring-tailed coati, *N. nasua* (Hirsch 2011; Hirsch and Gompper in press). One other procyonid genus, the mountain coati (*Nasuella*), forms female groups, though data on philopatry are lacking (Balaguera-Reina et al. 2009). Female philopatry characterizes raccoons (Gehrt and Fritzell 1998b; Dharmarajan et al. 2009), but the reverse is reported for kinkajous (Kays et al. 2000; Kays and Gittleman 2001).

Like their counterparts in Panama, male coatis in CNM disperse socially as yearlings and remain solitary as adults. Males also leave their natal groups in both ring-tailed and mountain coatis (Beisiegel and Mantovani 2006; Hirsch 2011). After dispersal, males are markedly aggressive to each other in most Procyonidae (though weak male–male affiliation can occur in raccoons and kinkajous—Gehrt and Fritzell 1998a; Kays and Gittleman 2001). This aspect of dispersal may be constrained by phylogenetic history, but dispersal distances show more interpopulation variation. Our data support the idea that the short dispersal distances of males found on Barro Colorado Island reflect limited dispersal opportunities. A history of mild inbreeding there could reduce inbreeding depression, or selection might favor forays as an inbreeding avoidance mechanism more strongly when dispersal options are restricted (Perrin and Goudet 2001).

Though CNM females ranged widely, we did not find the affiliation between males and female bands predicted by Booth-Binczik et al. (2004) when females are difficult to defend. The data clearly reinforce the generalization that male–female association is rare (Gompper and Krinsley 1992). Aggressiveness of females toward males is nearly universal in white-nosed coatis (Gompper 1996), but in contrast, wherever they have been studied, female ring-tailed coatis show selective tolerance. Most male ring-tailed coatis remain solitary, but bands allow association with a single male year-round (Hirsch 2011). Thus, our data are consistent with Hirsch and Gompper's (in press) suggestion of phylogenetic constraints, though for this trait the constraints seem evolutionarily more recent.

Dalerum (2007), asking whether sociality has arisen repeatedly during the phylogenetic history of carnivores, could not resolve this question for Procyonidae. Our results suggest a possible reason: “sociality” is not a single trait, but rather the sum of many individual predispositions which phylogeny constrains to different degrees. Among coatis, ranging, group size and cohesion, and dispersal distances are evolutionarily labile. However, core aspects of the social system, in particular female philopatry, female affiliation with adult daughters except during the period of parturition, and female intolerance of males, have deeper phylogenetic roots.

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