

Christine C. Hass · David Valenzuela

## Anti-predator benefits of group living in white-nosed coatis (*Nasua narica*)

Received: 21 November 2001 / Revised: 17 January 2002 / Accepted: 12 January 2002 / Published online: 27 March 2002  
© Springer-Verlag 2002

**Abstract** Predation is often considered an important factor in the evolution of sociality among animals. We studied mortality patterns and grouping behavior of white-nosed coatis (*Nasua narica*) at sites in southern Arizona, USA, and western Jalisco, México. Coatis were monitored by radio-tracking and recaptures for more than 3 years at each site. In both populations, predation by large felids, including jaguars (*Panthera onca*) and pumas (*Puma concolor*), accounted for more than 50% of mortality of adult coatis. Predation rates were significantly higher on solo coatis than on coatis in groups at both study sites. Predation rates were negatively related to group size in Arizona. However, mortality of juveniles, as measured by the ratios of juveniles to adult females, was not related to the number of adult females per group in Arizona or Jalisco. Coatis exhibit a suite of behaviors, including foraging with the juveniles in the center of the group, sharing vigilance, alarm calling, mobbing and attacking predators, and a highly synchronous birth season, that are all consistent with the hypothesis that predation has played an important role in shaping coati social behavior.

**Keywords** *Nasua narica* · Predation · Group living · Survival analysis · Radio-telemetry

### Introduction

Protection from predation is considered a driving force for the development of sociality in many species (e.g., Alexander 1974; Bertram 1978; Wilson 1980; Taylor 1984; Rood 1986; Hill and Dunbar 1998; Janson 1998). Group living also may have foraging benefits, including increasing foraging or food-capture efficiency, and increasing the ability to usurp resources from solitary individuals or smaller groups (Vine 1971; Wilson 1980; Clark and Mangel 1986; Gompper 1996).

Individual animals living in groups may obtain anti-predator benefits such as increasing the ability to detect predators, cooperating in defense, providing more targets to the predator (dilution effect or predator confusion), using other animals as shields (selfish herd effect), and by reducing the probability of encountering a predator through clumping (Hamilton 1971; Vine 1971; Jarman 1974; Estes 1976; Bertram 1978; Wilson 1980; Pulliam and Caraco 1984; Taylor 1984). Group living may also have significant costs, including interference competition, increased disease and parasite transmission, and increased detectability of multiple animals compared to solitary animals (Taylor 1979; Wrangham et al. 1993; Côté and Poulin 1995; Janson and Goldsmith 1995; Valenzuela et al. 2000).

The order Carnivora encompasses a large range of body sizes and social organizations, from those that are solitary outside of reproductive periods, to those in large, closely-related groups (Bekoff et al. 1984). Carnivores may benefit from group living for prey acquisition (e.g., African lions *Panthera leo*; gray wolves *Canis lupus*: Gittleman 1989); or to obtain anti-predator benefits, as described above (e.g., mongooses Viverridae: Rood 1986; Clutton-Brock et al. 1999; African lions: Packer et al. 1990).

Adults of most species of the family Procyonidae are solitary outside of the mating season. Coatis (*Nasua*

Communicated by S. Krackow

C.C. Hass  
US Army Garrison, ATZS-ISB (Wildlife),  
Fort Huachuca, AZ 85613-6000, USA

D. Valenzuela (✉)  
Instituto de Ecología, UNAM, A.P. 70-270, Ciudad Universitaria,  
D.F., C.P. 04510, México  
e-mail: dvalen@buzon.uaem.mx  
Tel.: 52 777 3297019  
Fax: 52 777 3297019

*Present addresses:*  
C.C. Hass, Audubon Appleton-Whittell Research Ranch,  
HC 1 Box 44, Elgin, AZ 85611, USA

D. Valenzuela, CEAMISH,  
Universidad Autónoma del Estado de Morelos,  
Av. Universidad No. 1001, Col. Chamilpa, Cuernavaca,  
Morelos, C.P. 62210, México

spp.) are a notable exception, with adult females and subadults and juveniles of both sexes living in closely related groups of 5–40 individuals (Kaufmann 1962; Gompper 1995; Gompper and Decker 1998). Males leave their natal groups at sexual maturity (approximately 2 years of age) to take up a solitary existence. Adult males will join groups for brief periods during the annual 2–4 week mating period. Females leave groups to give birth in isolation and remain apart from the group, foraging alone, for 6–8 weeks until their offspring are mobile (Kaufmann 1962). The diet of coatis consists primarily of fruit and terrestrial invertebrates (Kaufmann 1962; Russell 1982; Saénz 1994; Gompper 1996; Valenzuela 1998). Possible benefits of group living for white-nosed coatis (*Nasua narica*) include protection from predation or infanticide (Russell 1982; Burger and Gochfeld 1992), and increased competitive ability of groups of females against larger males for locally-rich food sources (Gompper 1996). Several of the previous studies were conducted on Barro Colorado Island in Panama, where large felids were absent or very rare during the studies (Russell 1981; Gompper 1995).

Known predators of adult or juvenile coatis include jaguars (*Panthera onca*), pumas (*Puma concolor*), ocelots (*Leopardus pardalis*), boa constrictors (*Boa constrictor*), red-tailed hawks (*Buteo jamaicensis*), golden eagles (*Aquila chrysaetos*), capuchins (*Cebus capuchinus*), and humans (Risser 1963; Janzen 1970; Gilbert 1973; Mondolfi 1982; Newcomer and DeFarcy 1985; Rabinowitz and Nottingham 1986; Tewes and Schmidly 1987; Fedigan 1990; Russell 1991; Vickers 1991; Aranda 1993; Hoogesteijn et al. 1993; Jorgenson and Redford 1993; Perry and Rose 1994; Nuñez 1999). No studies to date, however, have quantified predation rates on coatis.

The purpose of this study was to examine the potential role of predation in the social organization of coatis. We compare predation rates and group sizes in two populations with different complements of predators, including big cats. This study focused on the relationship between sociality and predation in coatis. We attempt to answer the following questions: (1) What are the major sources of mortality of white-nosed coatis in these areas? (2) Do predation rates decrease with increasing group size? (3) Do mortality rates of juveniles and subadults decrease with an increase in the number of adult females in the groups? If grouping by adult female coatis confers significant anti-predator benefits, we expect predation rates to be inversely related to group size.

## Methods

### Study areas and populations

Field work was conducted in the Huachuca Mountains in southern Arizona, USA, and in the Chamela-Cuixmala Biosphere Reserve in western Jalisco, Mexico. The Huachuca Mountains are located about 120 km SE of Tucson, Arizona. The study area encompassed the northeastern quarter of the Huachuca Mountains (31°25′–31°35′ N, 110°16′–110°26′ W). Climate within the study area is semi-arid, and vegetation is primarily Madrean woodland

(*Quercus*, *Pinus*, *Juniperus*), with chaparral and grassland at lower elevations. Potential predators of coatis in the study area included pumas, bobcats (*Lynx rufus*), golden eagles, red-tailed hawks, spotted owls (*Strix occidentalis*), and black bears (*Ursus americanus*). Historically, jaguars, ocelots, and grizzly bears (*Ursus arctos*) also were found in the area (Hoffmeister 1986).

The Chamela-Cuixmala Biosphere Reserve is located on the coast of Jalisco, 100 km north of Manzanillo and 140 km south of Puerto Vallarta (19°22′–19°35′ N, 104°56′–105°03′ W). The habitat consists of tropical dry forest (*Amphipterygium*, *Bursera*, *Caesalpinia*, *Ceiba*, *Cordia*, *Ficus*, *Spondias*) with some adjacent agricultural lands. Potential predators included jaguars, pumas, ocelots, boa constrictors, red-tailed hawks, common black hawks (*Buteogallus anthracinus*), great black hawks (*Buteogallus urubitinga*), and gray hawks (*Buteo nitidus*). In both Arizona and Jalisco, study animals were not habituated to humans, and were difficult to observe in the dense vegetation.

### Capture methods

We captured coatis in Tomahawk live-traps between January 1996 and December 1999 in Arizona, and between November 1994 and March 1997 in Jalisco. We immobilized captured animals with ketamine hydrochloride at 16 mg/kg, or a mixture of ketamine hydrochloride and xylazine hydrochloride at 22 mg/kg (Seal and Kreeger 1987), recorded standard morphometrics, and marked them with colored plastic eartags. We fitted adult coatis with radio-collars equipped with mortality or activity sensors (Advanced Telemetry Systems; Wildlife Materials). In Arizona, some coatis were marked with colored nylon collars to facilitate identification at a distance. The general health of each animal was recorded, and, in Jalisco, a condition score was assigned based on the degree of mite (*Notoedres*) infestation (Valenzuela et al. 2000). Trapping and handling protocols were designed to minimize stress to captured animals (ad hoc Committee for Acceptable Field Methods in Mammalogy 1987).

### Radio-telemetry and monitoring of survival

We monitored coatis from January 1996 through July 2000 in Arizona and from November 1994 through April 1998 in Jalisco. We attempted to locate radio-collared coatis at least twice per week. Approximately monthly in Arizona, radio-collars were used to locate groups, which were then approached to attempt to count marked individuals. When mortalities of radio-collared animals were suspected (from changes in mortality or activity sensors), we located the remains as quickly as possible and took detailed notes and photographs of the area. Frequent monitoring resulted in recovery usually within 24–72 h of death; in two cases 1–2 weeks elapsed before a carcass was recovered. Only coatis with active radio-collars could be confirmed dead; other marked animals and those whose radio-collar batteries had expired were recorded as disappearances (censored) at their last recorded observation.

We examined whole carcasses for signs of predation; if none was found the carcass was submitted to local veterinarians for necropsy. If predation was indicated, we assigned likely predators based on recovered remains (O’Gara 1978; Wade and Bowns 1981; Shaw 1987). We ascribed mortality to black bear predation if the hide was mostly intact and inverted over the pectoral girdle and head. The lack of talon punctures in the hide, the intact skull, and the pattern of hide inversion distinguished this from predation or scavenging by hawks, eagles, or vultures (Wade and Bowns 1981). We ascribed mortality to felid predation if the remains consisted of a pile of hair, with few bones remaining except the terminal 10–20 cm of tail, the mandible, and the maxilla, nasal, and occasionally the frontal bones. On occasion, one or two paws or portions of the respiratory or gastrointestinal tracts might be present, but usually most of the carcass was consumed. The amount of material remaining, and activity of radio-collared jaguars and pumas (monitored by colleagues, e.g., Nuñez 1999) in the area were used to separate jaguar from puma predation in Jalisco.

### Calculation of adult survival and mortality rates

We illustrated survival functions of adults between sexes and study areas using the Kaplan-Meier survival function with staggered entry (White and Garrott 1990; Pollock et al. 1989). We calculated survival and mortality rates as a function of time monitored (number of deaths per animal-day). Two or four periods were used for calculation of predation rates, based on behavioral changes related to reproduction. For males, the mating period encompassed the 4–6 weeks surrounding the peak conception period; the non-mating period included the rest of the year. For females, the reproductive period included the mating period, the gestation period, and the nesting period during which females were away from the group while their neonates remained in nests or dens. The non-reproductive period included the 7.5 months in between reproductive periods. This method allowed us to account for variable monitoring times on individual coatis during different periods. We included in the denominator all radio-collared adults, as well as all recognizable adults observed for at least 4 months, by status, i.e., male vs female, group vs solo, etc. We recorded duration of monitoring from the first date that animals were marked. Surviving animals were censored on the last date a signal was received from the transmitter, or the animal was observed, or the last date of the study if it was known to still be alive at the end of the study.

We calculated daily survival rate (DSR) as:

$$DSR_i = (\text{coati} - \text{days}_i - \text{total deaths}_i) / \text{coati} - \text{days}_i$$

where  $i$  refers the interval being considered (Heisey and Fuller 1985). We calculated daily mortality rates (DMR) as:

$$DMR_i = \text{deaths}_i / \text{coati} - \text{days}_i$$

[the Mayfield estimator (Heisey and Fuller 1985; Krebs 1989; Bart et al. 1998)]. Daily predation rates (DPR) were the number of deaths due to predation/coati-days. We calculated interval rates as:

$$ISR_i = DSR_i^{L_i}$$

$$IPR_i = \left( \frac{DPR_i}{1 - DSR_i} \right) (1 - ISR_i)$$

where  $ISR_i$  = the survival rate during interval  $i$ ,  $L_i$  is the length of interval  $i$ , and  $IPR_i$  = the predation rate during interval  $i$  (Heisey and Fuller 1985). Asymmetric 95% confidence intervals for survival and mortality rates were calculated as:

$$\ln R \pm z_{\alpha/2} R^{-1} \text{SE}(R)$$

where  $R$  is the estimated rate,  $z_{\alpha/2}$  is the appropriate standard normal value, and  $\text{SE}(R)$  is the standard error of the rate calculated using the Taylor series approximation (Heisey and Fuller 1985). We compared daily predation rates between sexes and periods using an exact binomial test, with  $n=a+b$ , and  $P=T_1/(T_1+T_2)$  (Rothman 1986; StataCorp 1997), where  $a$  = deaths due to predation in group 1,  $b$  = deaths due to predation in group 2,  $T_1$  = observation time on group 1, and  $T_2$  = observation time on group 2. In this instance, "group" refers to animals in a particular class, i.e., male or female, group or solo, etc. Binomial probabilities were calculated for  $a \geq n^*P$ , given that  $a > n^*P$ , for one-tailed tests and doubled for two-tailed tests. We used one-tailed  $P$ -values to test our major prediction that predation would be higher on smaller groups or solo coatis. All other tests were two-tailed, with  $\alpha=0.05$ .

### Group sizes and juvenile survival

We measured group sizes at our study sites 3–5 months after parturition. In Arizona, group sizes were obtained from observations of radio-collared coatis and their associated groups. In Jalisco, group sizes were obtained during walking censuses of the study area (Valenzuela 1998). Censuses in Jalisco were of groups not containing radio-collared animals; therefore these particular groups could not be followed to determine predation rates. We excluded cases in which we knew, from individually recognizable

animals, that two groups were together. We counted the number of adult females, yearlings, and juveniles in groups. We estimated early juvenile survival from the ratio of juveniles to adult females, assuming an average litter size of wild-born coatis of four (Pratt 1962; Risser 1963; Valenzuela 1998). Pregnancy rates approached 100% (C.C. Hass, unpublished data); for calculation purposes, we assumed that all adult females gave birth. Survival to 15–17 months was determined from ratios of yearlings to adult females. Females seldom leave their natal groups, and males do not disperse until they are over 2 years old (Gompper 1997), so all loss of juveniles and yearlings should be due to mortality. In most cases, it was difficult to distinguish yearlings older than 18 months from older animals, so no attempt was made to look at attrition of other age classes. We used linear regression to examine the relationship of juvenile and yearling survival to the number of adult females in the groups. A log-transformation of the dependent variable was used to normalize the data. Data from groups observed for more than 1 year were averaged, so that each group was represented only once in each data set. We expected that groups with more adult females would exhibit higher ratios of juveniles and yearlings to adult females, as a result of reduced predation. We used linear regression to compare predation rates to group sizes and number of adult females, averaged over years for each group in Arizona. Square-root transformations were used on both independent and dependent variables to normalize data and improve the fit of the regression line.

## Results

Seventy-three coatis were captured in Arizona, including 17 adult males, and 39 adult females. This sex ratio differed significantly from 1:1 (binomial test,  $P=0.0046$ ). Fifty coatis were monitored, 38 by radio-tracking and the rest from recaptures and observations of marked animals, for 27,634 coati-days. Twenty-five radio-collared coatis died during the study, including 17 killed by felids, one killed by a black bear, and one killed by an unknown predator. Additional causes of mortality of radio-collared animals included canine distemper virus, accidental trauma (possibly due to falling from a tree), one trapping-related death, and three due to unknown causes. Predation accounted for  $\geq 76\%$  of mortalities of radio-collared animals. Additional sources of mortality of unmarked coatis during the study included predation by felids ( $n=5$ ), black bears ( $n=1$ ), spotted owls ( $n=1$ ), domestic dogs ( $n=3$ ); plus four coatis killed by vehicles, and one killed by electrocution at an electrical substation. These latter mortalities were recovered opportunistically, and not included in any analyses.

One hundred forty-six coatis were captured in Jalisco, including 26 adult males and 54 adult females. This sex ratio differed significantly from 1:1 (binomial test,  $P=0.0023$ ). Thirty-two coatis were monitored, 18 by radio-tracking and the rest by recaptures for 9,210 coati-days. Eleven marked coatis died during the study, including six killed by predators, two that died from complications from scabies (*Notoedres cati*) infestation, one that died from dehydration or starvation, and two that died from unknown causes. Predation accounted for  $\geq 55\%$  of mortalities of radio-collared animals. All radio-collared animals that were killed by predators had no visible mite infestation. Additional sources of mortality of unmarked coatis included 39 animals that were euthanized to re-



**Table 1** Annual survival and cause-specific mortality rates for white-nosed coatis (*Nasua narica*) in Arizona, USA, and Jalisco, Mexico. Parentheses enclose 95% confidence intervals; see text for calculations. No male coatis were radio-tracked in Arizona during 2000

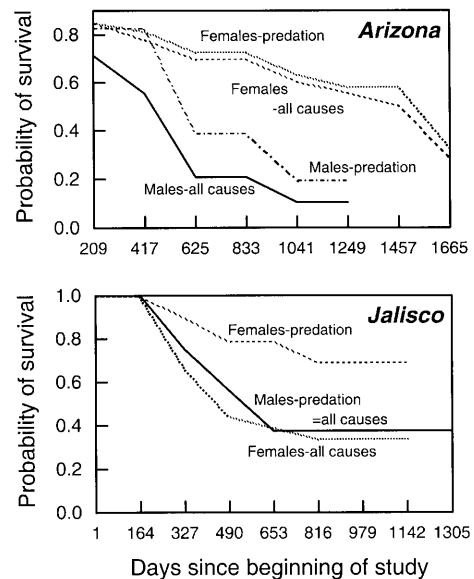
Site	Year	Sex	Number monitored	Number died	Number censored	Coati-days	Interval rates		
							Survival	Mortality	
								Predation	Other
Jalisco	1994	Male	1	0	0	60	1.0	0	0
		Female	3	0	0	166	1.0	0	0
	1995	Male	6	1	2	1,048	0.71 (0.36–1.0)	0.29 (0–0.78)	0
		Female	19	6	6	2,829	0.46 (0.25–0.86)	0.18 (0–0.40)	0.36 (0.08–0.64)
	1996	Male	6	2	1	1,158	0.53 (0.22–1.0)	0.47 (0.003–0.93)	0
		Female	11	2	6	2,469	0.7433 (0.49–1.0)	0.13 (0–0.36)	0.13 (0–0.36)
	1997	Male	3	0	2	599	1.0	0	0
		Female	3	0	2	708	1.0	0	0
	1998	Male	1	0	1	119	1.0	0	0
		Female	1	0	1	54	1.0	0	0
Arizona	1996	Male	11	4	0	2,257	0.53 (0.29–0.99)	0.12 (0–0.33)	0.35 (0.03–0.67)
		Female	28	4	0	5,849	0.78 (0.62–0.99)	0.16 (0–0.33)	0.05 (0–0.16)
	1997	Male	9	5	1	1,674	0.34 (0.13–0.87)	0.53 (0.18–0.88)	0.13 (0–0.37)
		Female	29	3	8	7,041	0.86 (0.77–1.0)	0.14 (0–0.29)	0
	1998	Male	5	1	2	532	0.50 (0.13–1.0)	0.50 (0–1.0)	0
		Female	12	2	6	3,604	0.86 (0.71–1.0)	0.14 (0–0.31)	0
	1999	Male	2	1	1	324	0.32 (0.04–1.0)	0.68 (0–1.0)	0
		Female	12	2	3	3,604	0.82 (0.62–1.0)	0.09 (0–0.27)	0.09 (0–0.27)
	2000	Female	7	3	4	1,319	0.62 (0.36–1.0)	0.38 (0.05–0.72)	0

duce a scabies epidemic (Valenzuela et al. 2000), one coati killed by a felid, one killed by an unknown predator, three killed by vehicles, and eight deaths from unknown causes (Valenzuela 1998).

Overall survival rates of adult coatis were 18% (95% CI: 6–35%) in Arizona and 35% (95% CI: 14–57%) in Jalisco (Fig. 1). In Arizona, annual survival rates ranged from 32% to 52% for adult male coatis and from 61% to 87% for adult female coatis (Table 1). Predators in Arizona killed 7 of 13 radio-collared male coatis, and 12 of 25 radio-collared female coatis. Of the female coatis killed by predators, seven were in groups, and five were isolated from the groups during the nesting seasons.

In Jalisco, annual survival rates ranged from 53% to 100% for adult males, and from 46% to 100% for adult females (Table 1). Predators in Jalisco killed 3 of 7 radio-collared male coatis, and 3 of 11 radio-collared female coatis. Of the females killed by predators, one was killed while in a group, the other two were killed while isolated from groups during the nesting season.

Daily predation rates were more than twice as high on male coatis as on female coatis in both populations (Arizona: male = 0.0015, female = 0.0005,  $P=0.0220$ ; Jalisco: male = 0.0010, female = 0.0005,  $P=0.1962$ ). Daily predation rates did not differ during reproductive (mating) versus non-reproductive periods for males in Arizona (reproductive = 0.0045, non-reproductive = 0.0010;  $P=0.0723$ ) or in Jalisco (reproductive = 0, non-reproductive = 0.0011;  $P=0.7318$ ). Daily predation rates were significantly higher during reproductive periods (mating, gestation, nesting) than non-reproductive periods for females in Arizona (reproductive = 0.0011, non-



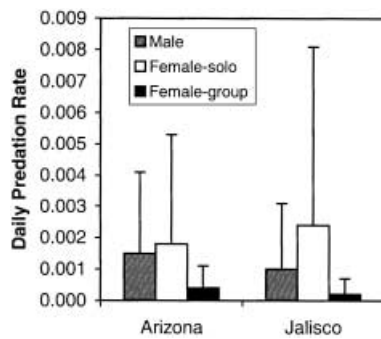
**Fig. 1** Kaplan-Meier survival curves for white-nosed coatis (*Nasua narica*) at study sites in Arizona, USA, and Jalisco, Mexico. See text for description of methods and non-predation mortality. Coatis were entered into the survival function on their day of capture

reproductive = 0.0001;  $P=0.0027$ ), but not in Jalisco (reproductive = 0.0007, non-reproductive = 0.0003;  $P=0.5371$ ).

Predation rates were 6.5–13 times higher for females during the nesting period, compared with the rest of the year, in both areas (Arizona: nesting = 0.0022, non-nesting = 0.0003;  $P=0.0023$ , one-tailed; Jalisco: nesting =

**Table 2** Survival and cause-specific mortality of white-nosed coatis during reproductive periods in Arizona and Jalisco

Site	Sex	Interval	Days in interval	Number killed by predators	Coati-days	Daily rates					
						Survival	95% CI	Mortality			
								Predation	95% CI	Other	95% CI
Jalisco	Male	Mate	30	0	295	1.0		0		0	
		Other	335	3	2,689	0.9989	0.9976–1.0	0.0011	0–0.0024	0	
	Female	Mate	30	0	660	0.9984	0.9955–1.0	0		0.0015	0–0.0045
		Gestation	61	0	1,373	0.9993	0.9978–1.0	0		0.0007	0–0.0022
		Nesting	46	2	830	0.9976	0.9943–1.0	0.0024	0–0.0057	0	
		Other	228	1	3,363	0.9988	0.9976–.9999	0.0003	0–0.0009	0.0009	0–0.0019
Arizona	Male	Mate	47	3	673	0.9896	0.9819–.9972	0.0045	0–0.0094	0.0059	0.0001–0.0118
		Other	318	4	4,113	0.9972	0.9956–.9989	0.0010	0–0.0020	0.0018	0.0005–0.0031
	Female	Mate	47	1	2,933	0.9997	0.9990–1.0	0.0003	0–0.0011	0	
		Gestation	56	4	3,803	0.9989	0.9979–.9999	0.0011	0–0.0021	0	
		Nesting	36	5	2,255	0.9973	0.9952–.9994	0.0022	0.0003–0.004	0.0004	0–0.0013
		Other	226	2	13,857	0.9998	0.9995–1.0	0.0001	0–0.0003	0.0001	0–0.0002

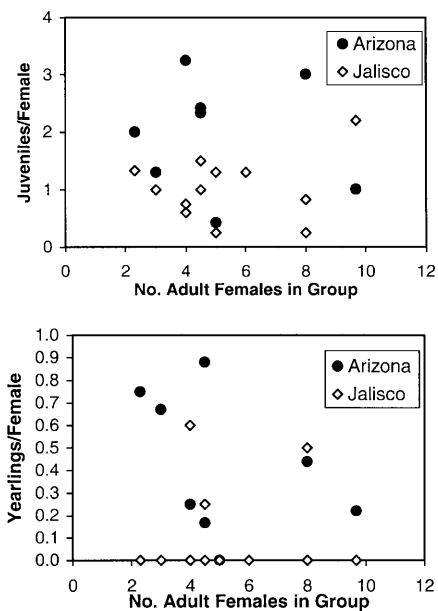


**Fig. 2** Daily predation rates (deaths per coati-day) of white-nosed coatis at Arizona and Jalisco study sites. Vertical bars represent 95% confidence limits. Females were solitary during 1–3 weeks prior to parturition and foraged alone for 5–6 weeks following parturition. They were with groups consisting of juveniles, sub-adults, and adult females for the remainder of the year. Males were considered solitary all year

0.0024, non-nesting = 0.0002;  $P=0.0255$ , one-tailed). Overall, solo animals (males all year and females during nesting periods) suffered significantly higher predation than females in groups (Arizona: solo = 0.0017, group = 0.0004,  $P=0.0007$ ; Jalisco: solo = 0.0013, group = 0.0002;  $P=0.0264$ , one-tailed; see Table 2, Fig. 2).

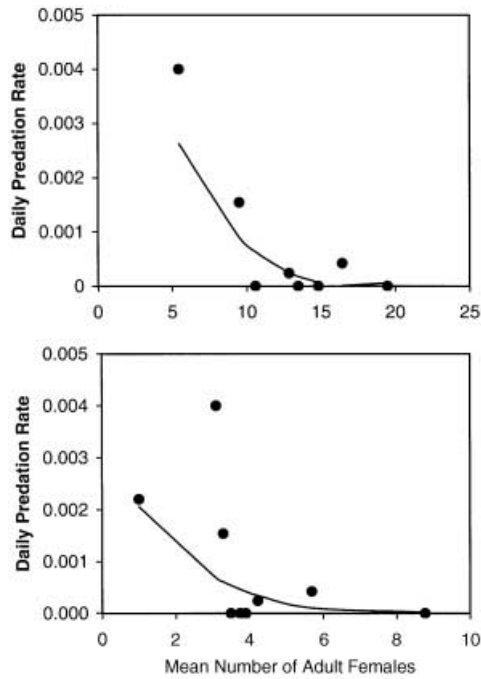
### Group sizes

Maximum group sizes did not differ significantly between populations ( $t$ -test for unequal variances,  $t=1.953$ ,  $P=0.082$ ), with mean ( $\pm$ SE) group sizes of  $17.0\pm 3.2$  coatis in Arizona ( $n$  groups = 8) and  $10.2\pm 1.3$  coatis in Jalisco ( $n$  groups = 12). The number of adult females per group ranged from 2 to 10, with 75% of groups having 3–7 females. The number of adult females per group did not differ between Arizona (mean =  $5.1\pm 0.9$ ,  $n$  groups = 8) and Jalisco (mean =  $5.0\pm 0.5$ ;  $n$  groups = 12,  $t=0.08$ ,  $P=0.940$ ).



**Fig. 3** Survival of juvenile (*top*) and yearling (*bottom*) white-nosed coatis by the number of adult females per group in Jalisco and Arizona. Group composition data were collected during the autumn, when juveniles were 3–5 months old, and yearlings were 15–17 months old

The average numbers of 3–5-month-old juveniles per adult female ranged from 1.0 in Jalisco to 2.3 in Arizona. This indicates early mortality rates of 43–75%, based on an average litter size of four (Pratt 1962; Risser 1963; Valenzuela 1998). The regression of juvenile survival on adult females was not significant in Arizona ( $\ln$ Juvenile survival =  $-0.02$  Females + 1.13,  $F=0.18$ ,  $df=1,6$ ,  $P=0.7532$ ,  $R^2=0.02$ ), nor in Jalisco ( $\ln$ Juvenile survival =  $-0.05$  Females + 0.90,  $F=1.06$ ,  $df=1,10$ ,  $P=0.3279$ ,  $R^2=0.10$ ; see Fig. 3). In other words, juvenile mortality appeared to be independent of group size in both populations. The average number of yearlings per adult female ranged from 0.1 in Jalisco to 0.5 in Arizona, indicating



**Fig. 4** Annual predation rates in groups of white-nosed coatis in the Huachuca Mountains, Arizona. *Top*, predation rates regressed on individual groups averaged over multiple years. Groups included adult females, juveniles, and subadults of both sexes. Predation rate =  $(-0.028\sqrt{\text{group size}} + 0.117)^2$ . *Bottom*, predation rates regressed against the average number of adult females in each group. Predation rate =  $(-0.025\sqrt{\text{females}} + 0.071)^2$

88–97% mortality by 17 months of age. The regression of yearling survival on adult females was not significant in Arizona ( $\ln\text{Yearling survival} = -0.03 \text{ Females} + 0.50$ ,  $F=0.97$ ,  $df=1,6$ ,  $P=0.3617$ ,  $R^2=0.14$ ), nor in Jalisco ( $\ln\text{Yearling survival} = 0.02 \text{ Females} - 0.03$ ,  $F=0.75$ ,  $df=1,10$ ,  $P=0.4053$ ,  $R^2=0.07$ ).

Annual predation rates were negatively related to group size in Arizona (Predation rate =  $(-0.28\sqrt{\text{group size}} + 0.117)^2$ ;  $F=9.32$ ,  $df=1,6$ ,  $P=0.0224$ ,  $R^2=0.61$ , 95% CI on coefficient =  $-0.051$  to  $-0.006$ ; see Fig. 4). A similar trend was observed between predation rate and the number of adult females per group, but the regression model was not significant (Predation rate =  $(-0.025\sqrt{\text{females}} + 0.071)^2$ ;  $F=3.13$ ,  $df=1,7$ ,  $P=0.121$ ,  $R^2=0.31$ ; 95% CI on coefficient =  $-0.059$  to  $0.009$ ; see Fig. 4). Group size data were difficult to obtain in Jalisco, thus it was not possible to calculate predation rates for groups of different sizes (see Methods). However, of four radio-collared females whose group sizes could be calculated, the only one killed by a predator was observed in a group with fewer than four adult females; the others were observed in groups of four or more adult females.

## Discussion

The results of this study are consistent with the hypothesis that group living provides significant anti-predator

benefits to adult coatis. Predation rates were significantly higher on solitary adults than on adults in groups, and higher on smaller groups than on larger groups. Predation rates were remarkably similar at both sites. However, it should be noted that due to the low number of coatis killed by predators in Jalisco, the power to detect differences between populations is low. Mortality rates on juveniles and yearlings were not related to group size in either population.

Large cats appeared to account for most of the adult coati mortality in this study. This study was also the first to suggest predation on coatis by black bears. The majority of deaths attributed to felid predation in the Huachuca Mountains, Arizona, were likely due to puma predation. Although coyotes (*Canis latrans*) were present at both study sites, none of the remains recovered suggested coyote predation, nor could we find any documentation of coyotes killing coatis. Recent sightings of jaguars have been made in southeastern Arizona, but no confirmed sightings have come from the Huachuca Mountains (Rabinowitz 1999). At this time, we believe jaguars to be too rare in Arizona to be significant predators on coatis. Coatis can be hunted legally in Arizona, however hunting of coatis was not permitted on Fort Huachuca during the study, and no marked coatis were reported to be taken by hunters.

In the Chamela-Cuixmala Biosphere Reserve, Jalisco, most of the deaths attributed to felid predation were likely due to jaguars, although one unmarked coati mortality appeared to be a puma kill. In a concurrent study of jaguar and puma food habits at Chamela-Cuixmala Biosphere Reserve, coatis made up 20% of the diet of jaguars; significantly more than in the diet of pumas (Nuñez 1999). Although bobcats have been reported recently from the Chamela-Cuixmala Biosphere Reserve (Lopez-Gonzalez et al. 1998), we believe them to be too uncommon to be significant predators on coatis in Jalisco. Hunting of coatis was not permitted in the reserve, and there was no evidence of poaching of coatis during the study.

Predation rates were 2–3 times as high on adult males than on adult females in both study sites. This bias in predation may have resulted in the sex-bias found among captured animals, in which we captured more than twice as many adult females as adult males at both sites. On Barro Colorado Island, Panama, with little or no predation on adult coatis, sex ratios of captured and observed free-roaming adults are approximately equal (Kaufmann 1962; Gompper 1997). Although sex-bias in trapped animals may represent a bias in trapability, we would expect such a bias to occur at all sites. Higher predation rates on male ungulates have been reported (e.g., Clutton-Brock et al. 1982; Owen-Smith 1993). Likewise, solitary Thompson's gazelles (*Gazella thomsoni*), both males and periparturient females, were more vulnerable to predation by cheetahs (*Acinonyx jubatus*) than were animals in groups (Fitzgibbon 1990).

Mortality on juveniles at both sites was very high. In Costa Rica, predation on nestling coatis by capuchins

was common (Newcomer and DeFarcy 1985; Fedigan 1990; Perry and Rose 1994), and included up to 100% of the juveniles in some groups (Saénz 1994). Capuchins do not occur in Jalisco or Arizona, and the sources of high juvenile mortality found in this study are unknown. Predation is a likely factor, though, as three juvenile coatis in Arizona were killed by a spotted owl, puma, and domestic dog, and remains of juvenile coatis were found in two bobcat scats (C.C. Hass, unpublished data). Juvenile coatis weigh 500–750 g when they return to the groups (Kaufmann 1962; Risser 1963; Valenzuela 1998), and 2–3 kg one year later (Valenzuela 1998), and therefore are vulnerable to attack by a wide range of predators.

The survival of juveniles and yearlings was not clearly related to group size. Resource availability may be a confounding factor here. Researchers in Panama have noted increased rates of disappearance of juveniles during dry periods, when food resources are scarce (Kaufmann 1962; Russell 1982). Groups of foraging coatis can make a considerable amount of noise while rustling in the leaf litter and turning over rocks, and emitting contact calls among adults and chattering of juveniles. To the human observer, larger groups make more noise than smaller groups (personal observations); this is probably noticeable to predators as well. However, without more detailed information on actual causes of mortality of young coatis, it is difficult to separate effects of nutrition and predation on possible group-size related mortality. Clutton-Brock et al. (1999) found that mortality of juvenile suricates (*Suricatta suricatta*) was inversely related to group size in populations in areas with abundant predators, but positively related to group size in areas with fewer predators.

Resource abundance and dispersion differed markedly among sites, resulting in large differences in density (about 1.2–2 coatis/km<sup>2</sup> in Arizona: Lanning 1976; C.C. Hass, unpublished data; 42.9/km<sup>2</sup> in Jalisco: Valenzuela 1998). Home range sizes of groups also differed markedly among populations (about 1,200 ha in Arizona: C.C. Hass, unpublished data; 383 ha in Jalisco: Valenzuela and Ceballos 2000). Thus, coatis appear to respond to differences in resource availability by adjusting density, but not the number of adult females per group.

Variability in total group size among the coati populations studied appeared to be due primarily to variations in juvenile survivorship. Because the number of juveniles and yearlings changes throughout the year, perhaps the best measure of group size is the number of adult females in the group. Although highly philopatric, adult female coatis have been observed emigrating between groups, and large groups occasionally split to form smaller groups (Russell 1982; Gompper 1997; Gompper et al. 1997). Presumably, females could adjust the size of their groups by separating when their group became too large, or joining other groups when their group became too small. Gompper et al. (1997) documented that coati groups were composed of primarily related, but also some unrelated, individuals indicating that groups will accept members of other groups.

Group sizes of coatis on Barro Colorado Island, the only place for which comparable data are available, varied from a median of 6 (range 2–15) during 1958–1960 (Kaufmann 1962), 10 (5–18) during 1974–1978 (Russell 1982), to 16 (6–26) during 1989–1995 (Gompper 1997). The median number of adult females per group also varied, from 2.5 to 6.0 (compared to 4.5 in Jalisco and 5.5 in Arizona). The island is relatively free of large predators (Glanz 1991; Wright et al. 1994), and no researchers working on coatis reported predation on any of their study animals [although Russell (1981) documented infanticide]. However, the high variability in group sizes, due partially to a disease outbreak during Kaufmann's study, precludes direct comparison with our data.

Coatis living in groups exhibit a suite of anti-predator behaviors. A coati's grizzled brown coat is quite cryptic in the shade of their forest habitat. Groups forage in an elliptical pattern, with the youngest animals in the center (Russell 1983). They share vigilance (Kaufmann 1962; Russell 1983; Burger and Gochfeld 1992), and communicate with a variety of contact and alarm vocalizations (Kaufmann 1962; Russell 1982, 1983). Alarm grunts [referred to as "ha ha" calls by Gilbert (1973)] and tail switching may function not only to communicate to the group (Kaufmann 1962), but also to let the predator know it has been detected (Harvey and Greenwood 1978; Hasson 1991). Group members have been observed mobbing and attacking predators (Janzen 1970; Russell 1983; Poglayen-Neuwall 1990). Coatis also exhibit highly synchronous birth seasons, with most births occurring during a 10–14 day period within a population (Kaufmann 1962; Pratt 1962; Russell 1982). Most females bring their offspring back into the group during a 1-week span (Kaufmann 1962). Among a variety of mammals, seasonal changes in food supply constrain reproduction to a certain time of year (Rutberg 1987; Ims 1990; Hass 1997). However, predation appears to have promoted highly synchronous birth seasons among numerous species, especially in the tropics (Estes 1976; Pulliam and Caraco 1984; Boinski 1987; Rutberg 1987; Ims 1990; Saénz 1994). It seems unlikely that this range of anti-predator behaviors would exist in the absence of strong selective pressure by predators.

An omnivorous diet, composed primarily of invertebrates and fruits, is correlated with group living in a number of carnivore species (Macdonald 1983; Bekoff et al. 1984; Rood 1986; Gittleman 1989). Coatis are consistent with this pattern, in which the dispersion of highly renewable, patchily distributed resources allows long-term associations among females (Waser 1981; Rood 1986; Valenzuela 1999), which benefit in terms of increased survivorship. A suite of cooperative behaviors, including allomaternal care (both allonursing and babysitting), allogrooming, shared vigilance and defense, and coalition formation, maintains strong ties among group members (Kaufmann 1962; Russell 1983; Gompper et al. 1997). Although group foraging may increase capture rates of small vertebrates encountered by coatis (Kaufmann 1962), overall, coatis may forage more efficiently when



solitary (Gompper 1996). Full-grown male coatis weigh 20–30% more than adult females (Risser 1963; Gompper 1996; Valenzuela 1998), and were observed usurping access to fruit trees from small groups of coatis, but not larger groups (Gompper 1996). Gompper (1994, 1996) hypothesized that a major benefit of group living in coatis was the ability to defend food patches against larger males. This hypothesis does not explain grouping at the northern part of the coatis' range, where foods are widely distributed and not defendable. However, if males benefit from increased feeding efficiency when alone, it might explain why males are solitary when doing so appears to increase their vulnerability to predation. While defining an optimal group size for coatis is premature (Pulliam and Caraco 1984), the number of adult females in a group may represent a trade-off between predator detection/deterrence, competition for food, and increased parasitism (Gompper 1994; Valenzuela et al. 2000).

**Acknowledgements** The Arizona Game and Fish Heritage Fund (195028) funded the study in Arizona and the Fort Huachuca Wildlife Office provided additional funding and logistical support. The staff of the Ramsey Canyon Nature Conservancy Preserve allowed access to the preserve and shared coati sightings. J. Roback, Dr. J. Kaufmann, M. Seidman, and M. Tuegel provided field assistance in Arizona. The Fundación Ecológica de Cuixmala A.C. and the Instituto de Ecología, Universidad Nacional Autónoma de México, provided logistical and financial support for the study in Jalisco. Additional financial support was provided by a doctoral scholarship from the National Council for Science and Technology (CONACYT), and grants from PADEP, Universidad Nacional Autónoma de México, and Idea Wild. C. Chavez, D. Biggins, and friends at the CCBR provided logistical and field support in Jalisco. We appreciate the criticisms of J. Kaufmann, M. Tuegel, S. Stone, and anonymous reviewers on previous versions of the manuscript. Research activities were conducted in compliance with current laws of each country.

## References

- ad hoc Committee on Acceptable Field Methods in Mammalogy (1987) Acceptable field methods in mammalogy: preliminary guidelines approved by the American Society of Mammalogists. *J Mammal* 68:1–18
- Alexander RD (1974) The evolution of social behavior. *Annu Rev Ecol Syst* 5:325–383
- Aranda M (1993) Hábitos alimentarios del jaguar (*Panthera onca*) en la reserva de la Biosfera de Calakmul, Campeche. In: Medellín RA, Ceballos G (eds) Avances en el Estudio de los Mamíferos de México, publicaciones especiales, vol 1. Asociación Mexicana de Mastozoología, Mexico City, pp 231–238
- Bart J, Fligner MA, Notz WI (1998) Sampling and statistical methods for behavioral ecologists. Cambridge University Press, New York
- Bekoff M, Daniels TJ, Gittleman JL (1984) Life history patterns and the comparative social ecology of carnivores. *Annu Rev Ecol Syst* 15:191–232
- Bertram BCR (1978) Living in groups: predators and prey. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell, Oxford, pp 221–248
- Boinski S (1987) Birth synchrony in squirrel monkeys (*Saimiri oerstedii*). *Behav Ecol Sociobiol* 21:393–400
- Burger J, Gochfeld M (1992) Effect of group size on vigilance in the coati, *Nasua narica*, in Costa Rica. *Anim Behav* 44:1053–1057
- Clark C, Mangel M (1986) The evolutionary advantages of group foraging. *Theor Popul Biol* 30:45–75
- Clutton-Brock TH, Guinness FE, Albon SD (1982) Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago
- Clutton-Brock TH, Gaynor D, McIlrath GM, Maccoll AD, Kansky R, Chadwick P, Manser M, Skinner JD, Bretherton PNM (1999) Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *J Anim Ecol* 68:672–683
- Côté IM, Poulin R (1995) Parasitism and group size in social animals: a meta-analysis. *Behav Ecol* 6:159–165
- Estes RD (1976) The significance of breeding synchrony in the wildebeest. *East Afr Wildl J* 14:135–152
- Fedigan LM (1990) Vertebrate predation in *Cebus capuchinus*: meat eating in a neotropical monkey. *Folia Primatol* 54:196–205
- Fitzgibbon CD (1990) Why do hunting cheetahs prefer male gazelles? *Anim Behav* 40:837–845
- Gilbert B (1973) Chulo: a year among the coatimundis. Alfred A. Knopf, New York
- Gittleman JL (1989) Carnivore group living: comparative trends. In: Gittleman JL (ed) Carnivore behavior, ecology, and evolution. Cornell University Press, Ithaca, N.Y. pp 183–207
- Glanz WE (1991) Mammalian densities at protected versus hunted sites in central Panama. In: Robinson JG, Redford KH (eds) Neotropical wildlife use and conservation. University of Chicago Press, Chicago, pp 163–173
- Gompper ME (1994) The importance of ecology, behavior, and genetics in the maintenance of coati (*Nasua narica*) social structure. PhD thesis, The University of Tennessee, Knoxville, Tenn.
- Gompper ME (1995) *Nasua narica*. *Mamm Species* 487:1–10
- Gompper ME (1996) Sociality and asociality in white-nosed coatis (*Nasua narica*): foraging costs and benefits. *Behav Ecol* 7:254–263
- Gompper ME (1997) Population ecology of the white-nosed coati (*Nasua narica*) on Barro Colorado Island, Panama. *J Zool* 241:441–455
- Gompper ME, Decker DM (1998) *Nasua nasua*. *Mamm Species* 580:1–9
- Gompper ME, Gittleman JL, Wayne RK (1997) Genetic relatedness, coalitions and social behaviour of white-nosed coatis, *Nasua narica*. *Anim Behav* 53:781–797
- Hamilton WD (1971) Geometry for the selfish herd. *J Theor Biol* 31:295–311
- Harvey PH, Greenwood PJ (1978) Anti-predator defense strategies: some evolutionary problems. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell, Oxford, pp 129–151
- Hass CC (1997) Seasonality of births in bighorn sheep. *J Mammal* 78:1251–1260
- Hasson O (1991) Pursuit-deterrent signals: communication between prey and predator. *Trends Ecol Evol* 6:325–329
- Heisey D, Fuller T (1985) Evaluation of survival and cause-specific mortality rates using telemetry data. *J Wildl Manage* 49:668–674
- Hill RA, Dunbar RIM (1998) An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. *Behaviour* 135:411–430
- Hoffmeister DF (1986) Mammals of Arizona. University of Arizona Press, Tucson, Ariz.
- Hoogsteijn R, Hoogsteijn A, Mondolfi E (1993) Jaguar predation and conservation: cattle mortality caused by felines on three ranches in the Venezuelan Llanos. *Symp Zool Soc Lond* 65:391–407
- Ims R (1990) The ecology and evolution of reproductive synchrony. *Trends Ecol Evol* 5:135–140
- Janson CH (1998) Testing the predation hypothesis for vertebrate sociality: prospects and pitfalls. *Behaviour* 135:389–410
- Janson CH, Goldsmith ML (1995) Predicting group size in primates: foraging costs and predation risks. *Behav Ecol* 6:326–336



- Janzen D (1970) Altruism by coatis in the face of predation by boa constrictor. *J Mammal* 51:387–389
- Jarman PJ (1974) The social organization of antelope in relation to their ecology. *Behaviour* 48:215–267
- Jorgenson JP, Redford KH (1993) Humans and big cats as predators in the neotropics. *Symp Zool Soc Lond* 65:367–390
- Kaufmann JH (1962) Ecology and social behavior of the coati, *Nasua narica*, on Barro Colorado Island, Panama. *Univ Calif Publ Zool* 60:95–222
- Krebs CJ (1989) *Ecological methodology*. Harper and Row, New York
- Lanning DV (1976) Density and movements of the coati in Arizona. *J Mamm* 57:609–611
- Lopez-Gonzalez CA, Gonzalez-Romero A, Laundre JW (1998) Range extension of the bobcat (*Lynx rufus*) in Jalisco, Mexico. *Southwest Nat* 43:103–105
- Macdonald DW (1983) The ecology of carnivore social behavior. *Nature* 301:379–384
- Mondolfi E (1982) Notes on the biology and status of the small wild cats in Venezuela. In: Miller SD, Everett DD (eds) *Cats of the world: biology, conservation, and management*. National Wildlife Federation, Washington, D.C. pp 125–146
- Newcomer MW, DeFarcy DD (1985) White-faced capuchin (*Cebus capuchinus*) predation on a nestling coati (*Nasua narica*). *J Mammal* 66:185–186
- Núñez R (1999) Hábitos alimentarios del jaguar (*Panthera onca*, Linnaeus 1758) y del puma (*Puma concolor*, Linnaeus 1771) en la Reserva de la Biosfera Chamela-Cuixmala, Jalisco, Mexico. Thesis, Universidad Michoacana de San Nicolas Hidalgo, Morelia, Mexico
- O’Gara BW (1978) Differential characteristics of predator kills. *Proc Antelope States Workshop* 8:380–393
- Owen-Smith N (1993) Comparative mortality rates of male and female kudus: the costs of sexual size dimorphism. *J Anim Ecol* 62:428–440
- Packer C, Scheel D, Pusey AE (1990) Why lions form groups: food is not enough. *Am Nat* 36:1–19
- Perry S, Rose L (1994) Begging and transfer of coati meat by white-faced Capuchin monkeys, *Cebus capuchinus*. *Primates* 35:409–415
- Poglayen-Neuwall I (1990) Coatis (Genera *Nasua* and *Nasuella*). In: Grzimek B, (ed). *Grzimek’s encyclopedia of mammals*. McGraw-Hill, New York, pp 461–464
- Pollock KH, Winterstein SR, Bunck CM, Curtis PD (1989) Survival analysis in telemetry studies: the staggered entry design. *J Wildl Manage* 53:7–15
- Pratt JJ (1962) Establishment and trends of coati-mundi in the Huachucas. *Mod Game Breeding* 23:10–11, 15
- Pulliam HR, Caraco T (1984) Living in groups: is there an optimal group size? In: Krebs JR, Davies NB (eds) *Behavioural ecology: an evolutionary approach*. Sinauer, Sunderland, Mass. pp 122–147
- Rabinowitz AR (1999) The present status of jaguar (*Panthera onca*) in the southwestern United States. *Southwest Nat* 44:96–100
- Rabinowitz AR, Nottingham BG Jr (1986) Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. *J Zool* 210:149–159
- Risser SC Jr (1963) A study of the coati mundi *Nasua narica* in southern Arizona. Thesis, University of Arizona, Tucson, Ariz.
- Rood JP (1986) Ecology and social evolution of mongooses. In: Rubenstein DI, Wrangham RW (eds) *Ecological aspects of social evolution. Birds and mammals*. Princeton University Press, Princeton, N.J. pp 131–152
- Rothman KJ (1986) *Modern epidemiology*. Little, Brown, Boston, Mass.
- Russell JK (1981) Exclusion of adult male coatis from social groups and protection from predation. *J Mammal* 62:201–206
- Russell JK (1982) Timing of reproduction by coatis (*Nasua narica*) in relation to fluctuations in food resources. In: Leigh EG Jr, Rand AS, Windsor DM (eds) *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C. pp 413–431
- Russell JK (1983) Altruism in coati bands: nepotism or reciprocity? In: Wasser SK (ed). *Social behavior of female vertebrates*. Academic Press, New York, pp 263–290
- Russell P (1991) The iguana banquet (circa 1927). In: Carmony NB, Brown DE (eds) *Mexican game trails: Americans afield in old Mexico, 1866–1940*. University of Oklahoma Press, Norman, Okla. pp 211–227
- Rutberg AT (1987) Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. *Am Nat* 130:692–710
- Saénz JM (1994) *Ecología del pizote (Nasua narica) y su papel como dispersador de semillas en el bosque seco tropical, Costa Rica*. Thesis, Universidad Nacional de Costa Rica, Heredia, Costa Rica
- Seal US, Kreeger TJ (1987) Chemical immobilization of furbearers. In: Nowak M, Baker JA, Obbard ME, Mallach B (eds) *Wild furbearer management and conservation in North America*. Ministry of Natural Resources, Toronto, Ontario, pp 191–215
- Shaw HG (1987) *Mountain lion field guide*. (Special report no. 9) Arizona Game and Fish Department, Phoenix, Ariz.
- StataCorp (1997) *Stata statistical software: release 5.0*. Stata Corporation, College Station, Tex.
- Taylor RJ (1979) The value of clumping to prey when detectability increases with group size. *Am Nat* 113:299–301
- Taylor RJ (1984) *Predation*. Chapman and Hall, New York
- Tewes ME, Schmidly DJ (1987) The neotropical felids: jaguar, ocelot, margay, and jaguarundi. In: Nowak M, Baker JA, Obbard ME, Mallack B (eds) *Wild furbearer management and conservation in North America*. Ministry of Natural Resources, Toronto, Ontario, pp 697–711
- Valenzuela D (1998) Natural history of the white-nosed coati, *Nasua narica*, in the tropical dry forests of western México. *Rev Mex Mastozool* 3:26–44
- Valenzuela D (1999) Efectos de la estacionalidad ambiental en la densidad, la conducta de agrupamiento y el tamaño del área de actividad del coati (*Nasua narica*) en selvas tropicales caducifolias. PhD thesis, Universidad Nacional Autónoma de México, Mexico City
- Valenzuela D, Ceballos G (2000) Habitat selection, home range, and activity of the white-nosed coati (*Nasua narica*) in a Mexican tropical dry forest. *J Mammal* 81:810–819
- Valenzuela D, Ceballos G, Garcia A (2000) Mange epizootic in white-nosed coatis in western Mexico. *J Wildl Dis* 36:56–63
- Vickers WT (1991) Hunting yields and game composition over ten years in an Amazon Indian territory. In: Robinson JG, Redford KH (eds). *Neotropical wildlife use and conservation*. University of Chicago Press, Chicago, pp 53–81
- Vine I (1971) Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *J Theor Biol* 30:405–422
- Wade DA, Bowns JE (1981) Procedures for evaluating predation on livestock and wildlife. Texas Agricultural Extension Service, College Station, Tex.
- Waser PM (1981) Sociality or territorial defense? The influence of resource renewal. *Behav Ecol Sociobiol* 8:231–237
- White GC, Garrott RA (1990) *Analysis of wildlife radio-tracking data*. Academic Press, New York
- Wilson EO (1980) *Sociobiology*, abridged edn. Harvard University Press, Cambridge, Mass.
- Wrangham RW, Gittleman JL, Chapman CA (1993) Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behav Ecol Sociobiol* 32:199–209
- Wright SJ, Gompper ME, DeLeon B (1994) Are large predators keystone species in neotropical forests? The evidence from Barro Colorado Island. *Oikos* 71:279–294