

GOMPPER E. MATTHEW. CORRELATIONS OF COATI (*NASUA NARICA*) SOCIAL STRUCTURE WITH PARASITISM BY TICKS AND CHIGGERS, CAP. 42: 527-534. En: SÁNCHEZ-CORDERO V. y MEDELLÍN R.A. (Eds.) *CONTRIBUCIONES MASTOZOOLÓGICAS EN HOMENAJE A BERNARDO VILLA*, 666 p. Instituto de Biología e Instituto de Ecología, UNAM, México, 2004. ISBN 967-3422-44-9.

## 42. CORRELATIONS OF COATI (*NASUA NARICA*) SOCIAL STRUCTURE WITH PARASITISM BY TICKS AND CHIGGERS

MATTHEW E. GOMPPER

Department of Fisheries and Wildlife Sciences, University of Missouri,  
Columbia, Missouri 65211 U.S.A.

### Abstract

The contact rates of individuals within populations can vary considerably. How parasites respond to this variation is unclear. White-nosed coatis (*Nasua narica*) maintain a social structure of band-living females and solitary males. On coatis from Barro Colorado Island, Panama, the prevalence and intensity of two ectoparasites with similar transmission mechanism correlated differently between males and bands, and varied seasonally. Although tick (*Amblyomma ovale*) intensities were higher during the dry season versus wet season, there was no difference in the intensities of replete (blood engorged) and non-replete ticks on males and band members during the dry season. Males, however, had higher intensities and prevalences of non-replete and replete ticks than did band members during the wet season. The opposite pattern was observed for parasitism by chiggers (*Eutrombicula goeldii*). Band members had higher chigger prevalence than males. Chigger prevalence fluctuated greatly within bands and independently between bands. During any given period, however, almost all members of a band had chiggers or all did not. Females who briefly became solitary to give birth lost their chigger infestations, while males had increased prevalence of chiggers during the mating season when they briefly join bands. These data emphasize the possible influence of social structure in parasitism, and the importance of considering seasonal differences when examining the

### Resumen

role of host social structure on host-parasite interactions.

**Key words:** social structure, coati, *Ambylomma*, *Eutrombicula*, ectoparasites, seasonality

---

Social organization reflects evolutionary pressures to maximize fitness, and thus may help to avoid, minimize or eliminate parasitic infections. Cross-species studies suggest that parasites can exert selective pressures on host social structures (Davies et al., 1991; Hochberg, 1991) and intraspecific studies demonstrate positive correlations of group size, number of parasite species per host, and infection intensities (Keymer and Read, 1991; Møller et al., 1993). The general cause of these relationships is likely due to the increased social contact that occurs within groups, thus increasing opportunities for parasite transmission (Alexander, 1974; Freeland, 1979; Côté and Poulin, 1995; Porteous and Pankhurst, 1998). Sociality can also result in decreased parasitism if group-living species demonstrate behaviors such as grooming, or if group-living creates a dilution effect which decreases the chance of an individual being singled out by a vector or parasite (Freeland, 1977; Rubenstein and Hohmann, 1989; Mooring and Hart, 1992; Côté and Gross, 1993).

Whether an ectoparasite is positively or negatively influenced by host group-living is usually attributed to its life history, and especially its transmission mechanism and size (size influencing ease of removal from the host). However, few intraspecific studies have tested whether ectoparasite size and mode of transmission are robust predictors of the influence of host social structure on ectoparasite prevalence (the percent of hosts infected by a parasite; Bush et al., 1997) and intensity (number of parasites on a host; Bush et al., 1997). The contact rates of individuals within populations can vary greatly. In populations of some group-living species a substantial fraction of the population may live solitarily, and species commonly perceived as solitary may form ephemeral aggregations or show extensive spatial variability in sociality. This variability in contact among individuals may influence para-

---

site-host interactions. Using data collected on two ectoparasite species from a population of white-nosed coatis (*Nasua narica*), I examine the robustness of relationships between host social structure and parasite intensities, the prevalence of parasites in social groups, fluctuation in parasitism over time, and the size and mechanism of transmission of the parasite.

White-nosed coatis are 4 - 6 kg omnivores with a social structure unique within the Carnivora. Adult females and their immature offspring of < 2 years of age form permanent bands (Kaufmann, 1962), which at the study site include up to 26 individuals (mean = 15.3-Gompper, 1997). Adult females are highly philopatric and rarely leave the band except to give birth. In contrast, all adult males are solitary except for a brief (approximately two weeks) mating season. Because males are solitary regardless of female behavior, coatis are an ideal species for examining costs and benefits of group-living and asociality (Gompper, 1996; Gompper et al., 1997). In addition, cooperative interactions within bands (such as allogrooming, allonursing, and baby-sitting) are common. Band members are generally together during the day and sleep together in trees during the night. These behaviors, which are not observed among solitary males, may influence parasite intensity and prevalence.

I examine two types of coati ectoparasites: ticks and chiggers. Ticks are acquired as free-living organisms, and are not directly transmitted among individuals. They are attracted to hosts by a variety of stimuli such as CO<sub>2</sub> concentration, odor, heat, vibration and visual cues (Waladde and Rice, 1982), and become engorged by ingesting host blood and lymph. Engorgement therefore indicates an extended period of parasitism. Once satiated, the tick drops off its host and molts or lays eggs before finding a new host (Noble et al., 1989; Aeschlimann, 1991). A tick can be removed by the host by auto-

and allogrooming behaviors. Chiggers are free-living mites whose larvae are parasitic. Larvae are attracted to a host by increased levels of CO<sub>2</sub>, and tend to attach to hosts in closely packed clusters at a specific site such as the eye margin, anal area, or lateral edge of the ear, where they feed on digested host epidermal cells for several days (Sasa, 1961). The larvae then drop from the host and enter non-parasitic stages. Because of their small size (< 1 mm in length), chiggers are presumably more difficult to remove by grooming than are ticks.

Based on these similar mechanisms of transmission, and the behavior and social structure of the host, I test the hypothesis that social structure affects prevalence and intensity. Two predictions follow: (1) Replete (blood engorged) and non-replete tick prevalence and intensity is higher on solitary adult males than on band members because allogrooming among band members reduces the time a tick remains on its host; (2) Chiggers are presumably too small to remove by grooming, and thus, prevalence should be equal among social and asocial individuals.

## Study Area and Methods

I conducted field work on Barro Colorado Island (BCI), Panama, for 25 months between August 1989 and December 1995. BCI (9°9'N, 79°51'W) is a 15.6 km<sup>2</sup> island of tropical moist forest in Lake Gatun, an artificial body of water created during the building of the Panama Canal. Details on the population biology of the coati on BCI, and methods of trapping and handling are presented elsewhere (Wright et al., 1994; Gompper, 1997).

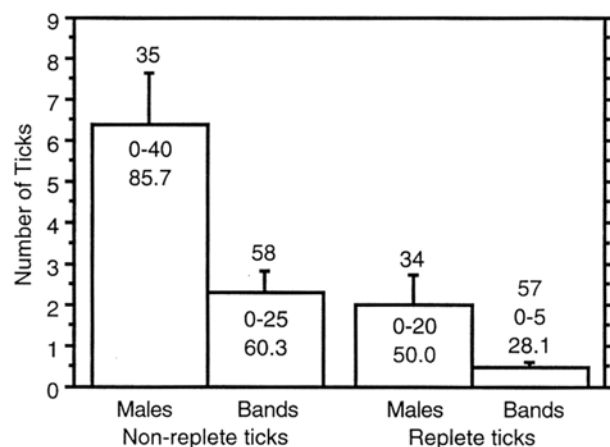
Coatis were trapped, anesthetized, and examined for ectoparasites. Information was collected on the total number of ticks, the number of replete ticks, the presence/absence of chiggers, and the region(s) of the body infested. Due to variation in susceptibility of individual coatis to the anesthetic, data sets for a few individuals were incomplete. Species of ticks reported from coatis in lowland, central Panama include *Amblyomma ovale*, *A. oblongoguttatum*, *A. naponense*, *A. cajennense*, *A. auricularium* and *Haemaphysalis juxtakochi*. Most ticks observed during this study were *A. ovale*, for which the coati may be a preferred host (Fairchild et al., 1966). Developmental stages of ticks were not assessed. Coatis in Panama may host several species of chigger, but

examination of chiggers collected from trapped individuals for this study revealed only *Eutrombicula goeldii* (Brennan and Yunker, 1966). Chigger infestations were easily identified on the host by a crusty, red inflammation around infected portions of the body, especially the lateral edge of the ear. The characteristic signs of chigger infestation (acariasis) also could be observed easily with binoculars on untrapped individuals. From March 1992 - December 1995 the identity, age, sex, and presence or absence of chigger infestation was recorded.

Data were pooled by season (wet and dry) and by social status for analyses of variance (ANOVA). Statistically significant differences existed in the variance of tick intensity of solitary males and social band members, and in the variance during the wet and dry seasons. This precluded the use of parametric analyses and Bonferroni corrections, so data were analyzed with nonparametric statistics. Comparisons of prevalence between age and sex classes was done using chi-squared tests, with juveniles and subadults of the same sex combined to minimize the number of cells with < 5 observations.

## Results

Individual coatis had greater intensities of non-replete ticks than replete ticks, with a higher prevalence of ticks on solitary males than on band members (Fig. 1). Age class did not affect the intensities of replete or non-replete ticks (Kruskal-



**Fig. 1.** Mean ( $\pm 1$  SE) intensity of non-replete and replete ticks found on trapped solitary adult male coatis and band members. Values represent sample sizes ( $n$ ), range, and prevalence (%), respectively.

**Table 1.** Prevalence (%) of ticks and chiggers on trapped band members, with sample size (n) in parentheses. Data are subdivided into age and sex classes.

	Adult females	Subadult males	Subadult females	Juvenile males	Juvenile females	<i>p</i>
Nonreplete ticks	52 (27)	53 (15)	86 (7)	83 (6)	33 (3)	0.566
Replete ticks	26 (27)	29 (14)	14 (7)	50 (6)	33 (3)	0.651
Chiggers	83 (23)	90 (10)	100 (6)	83 (6)	67 (3)	0.866

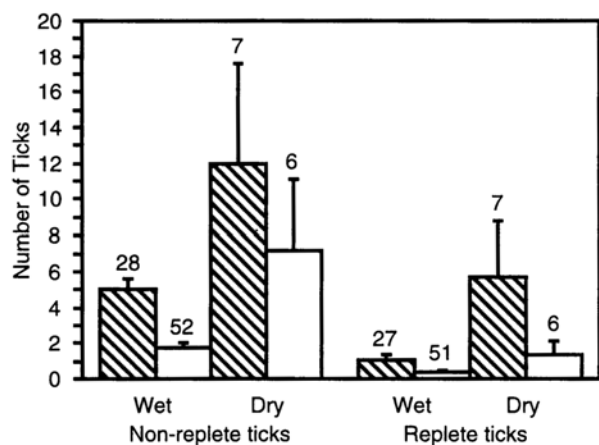
Wallis ANOVA *s* with *df* = 2; non-replete: *H* corrected for ties = 3.070, tied *p* = 0.216; replete: *H* corrected for ties = 1.843, tied *p* = 0.398), nor were there differences based on host sex (Mann-Whitney tests; non-replete: *U* = 330.0, tied *p* = 0.324; replete: *U* = 319.5, tied *p* = 0.285). The prevalence of ticks among different age and sex classes within bands also did not significantly differ (Table 1). Thus data on individuals from all age and sex classes within bands were lumped for comparisons with solitary adult males. Solitary males had significantly greater intensities of non-replete ticks (*U* = 478.0, tied *p* < 0.0001) and replete ticks than band members (*U* = 707.5, tied *p* = 0.0124) (Fig. 1).

This pattern varied temporally. During the wet season both non-replete and replete tick intensities and prevalence on coatis were less than during the dry season (non-replete: *U* = 331.5, tied *p* = 0.0334; replete: *U* = 354.0, tied *p* = 0.0431). Mean ( $\pm 1$  *SD*) wet and dry season intensities for non-replete ticks were  $2.89 \pm 3.07$  (*n* = 80; prevalence = 67.5%) and  $9.77 \pm 12.43$  (*n* = 13; prevalence = 84.6%), respectively. For replete ticks, mean wet and dry season intensities were  $0.62 \pm 1.20$  (*n* = 78; prevalence = 33.3%) and  $3.69 \pm 6.40$  (*n* = 13; prevalence = 53.8%), respectively.

Differences in tick intensities between solitary adult males and band members varied seasonally for both non-replete (*df* = 3, *H* corrected for ties = 21.969, tied *p* < 0.0001) and replete ticks (*df* = 3, *H* corrected for ties = 9.183, tied *p* = 0.0270) (Fig. 2). Post-hoc tests revealed that during the wet season, solitary males had significantly greater intensities of non-replete and replete ticks than band members (non-replete: *U* = 316.0, tied *p* < 0.0001; replete: *U* = 506.0, tied *p* = 0.0217). However, during the dry season when tick population densities were higher, there were no significant differences in the intensities of non-replete and replete ticks between solitary adult males and band members (non-replete:

*U* = 16.0, tied *p* = 0.4726; replete: *U* = 16.0, tied *p* = 0.4518). Although prevalence of parasitism by ticks was greater for males and band members during the dry season than the wet season (excluding non-replete ticks on males, for which prevalence rates are equal), the relative differences in prevalence between males and band members were greater during the wet season than during the dry season (Table 2).

Chiggers occurred on 71.6% of trapped coatis. Within bands there was no significant difference in the prevalence of chiggers among age classes and between males and females (Table 1), but the prevalence of chiggers varied significantly with the degree of host sociality (Fisher's exact test; *p* = 0.0007). Of 67 individuals trapped throughout the year, 48 (8 solitary males, 40 band members) had chiggers, and 19 (12 males, 7 band members) were free of chiggers (Table 2). Analyses of data from sightings of individuals where the presence or absence of chigger infestation was ascertained were

**Fig. 2.** Mean ( $\pm 1$  *SE*) intensity of non-replete and replete ticks found on trapped coatis, subdivided by social status and by season. Open bars indicate band members and hatched bars indicate solitary males. Sample sizes (*n*) are above error bars.

consistent with trapping results. This pattern was independent of the month of analysis (Table 3). Monthly prevalence ranged from 53 - 70%, with no significant difference between estimates made during wet season months and those made during dry season months ( $U = 8.5$ , tied  $p = 0.7110$ ). Yet for all months ( $n = 9$ ), the majority of band members were parasitized by chiggers, while for 8 of 9 months the majority of males were free of chiggers.

Prevalence of chiggers within bands fluctuated temporally and rapidly (Table 3). For example, prevalence among members of X band was 75% in March 1992, 0% in May 1992, and 92% in October 1992. Similarly, all members of T band observed in March 1992 were infected, but in July and November 1993 all individuals were free of chigger infections. In addition, the prevalence of chiggers among individuals in one band was apparently independent of that in a second, adjacent band (Table 3). For example, in November 1993 prevalence of X and T bands were 90% and 0%, although their respective home ranges overlapped extensively and individuals were often found at the same food sources during any particular day (Gompper, 1997). Home ranges of bands

KPLT, KL, and KB also overlapped, but prevalence among members of these bands varied greatly (0 - 100 %) during the months of July and October 1992. Similarly, during May 1992, all X band members were free of chigger infections, whereas all members (excluding solitary, parous females) of KPLT, KB, KL, and T bands were infected (Table 3).

Within bands, the prevalence of chiggers was skewed towards 0% or 100%. Of 38 non-independent band-months where > 3 individuals were examined for chigger presence/absence, almost half included entirely infected ( $n = 12$ ) or entirely uninfected ( $n = 6$ ) individuals. For an additional 11 band-months, chigger prevalence was either > 86% or < 25%. In contrast, among adult females who temporarily left the band to give birth in May, prevalence was low. Only one of eight solitary females (May 1992 in Table 3) was infected with chiggers, despite four of the chigger-free individuals having left entirely infected bands less than one month earlier. The binomial probability of this result occurring by chance when  $p_{presence} = 0.902$  and  $p_{absence} = 0.098$  (calculated from trapping data on band members) is  $p < 0.0001$ .

**Table 2.** Prevalence (%) of ticks and chiggers on solitary adult male coatis and band members trapped during the wet and dry season, with sample size (n) in parentheses.

	Non-replete ticks		Replete ticks		Chiggers	
	Wet	Dry	Wet	Dry	Wet	Dry
Males	86 (28)	86 (7)	48 (27)	57 (7)	39 (13)	43 (7)
Band members	58 (52)	83 (6)	26 (51)	50 (6)	90 (41)	50 (6)

**Table 3.** Monthly prevalence (%) of chiggers on coatis, with sample size (n) in parentheses. Data are subdivided by social structure (solitary males, band members, solitary females), with band members classified by social group. Sample sizes are the number of individuals closely examined (na = not applicable). Individuals not closely examined are not included. †Includes solitary females under their respective social group. †Excludes solitary females.

Date	Coati band													All bands	Solitary females
	males	kplt	x	kb	kl	t	gig	df	jvt	hood	ava	rsc	b		
Mar. 92	33 (6)	80 (5)	75 (8)		100 (3)	100 (4)	0 (3)							74 (23)	na
May 92 <sup>†</sup>	40 (5)	75 (4)	0 (9)	78 (9)	100 (3)	75 (4)								55 (29)	13 (8)
May 92 <sup>†</sup>	40 (5)	100 (3)	0 (7)	100 (7)	100 (3)	100 (2)								68 (22)	na
Jun. 92	33 (3)	100 (1)		67 (6)	50 (2)									67 (9)	na
Jul. 92	40 (5)	63 (8)		100 (8)	25 (4)	50 (2)								68 (22)	na
Oct. 92	38 (13)	100 (4)	92 (12)	86 (7)	0 (1)	50 (2)	67 (3)	100 (2)						84 (31)	na
Jul. 93	43 (7)	63 (8)	50 (4)	89 (9)		0 (4)			0 (2)					56 (27)	na
Nov. 93	40 (5)	92 (13)	90 (10)	100 (2)		0 (8)					100 (1)	100 (5)		74 (39)	na
Jan. 95	100 (4)	50 (4)	100 (13)		100 (8)	0 (2)							0 (3)	77 (30)	na
Dec. 95	44 (9)	56 (9)	64 (14)	80 (5)									100 (3)	63 (40)	na

## Discussion

These results support the hypothesis that intrapopulation variation in host social structure may influence the parasites found on an individual. Identifying the correlation is not straightforward, however, even with knowledge of the transmission mechanism of the parasite. As predicted, parasitism by ticks was greater on solitary males than on band members. The low prevalence of replete ticks on band members suggests that allogrooming within bands reduces tick intensities. Similarly, groups of *Peromyscus leucopus* that were experimentally infested with *Ixodes scapularis* had lower numbers of attached tick and lower numbers of replete ticks than single *P. leucopus* (Levin and Fish, 1998). Chiggers did not, however, parasitize solitary and social individuals equally. Rather, individuals living in groups had increased chigger burdens relative to solitary individuals. Thus, two species of parasites with similar mechanisms of transmission and similar host-seeking strategies had very different probabilities of being found on subsets of individuals (bands) within the host population because of the social structure of the host.

Problematically, sex and social structure are confounded for coatis. Several lines of evidence, however, suggest that host social structure is the more likely explanation for the observed patterns. First, the observation that temporarily solitary, lactating females lost their chigger infections suggests that group-living is important for chigger parasitism, independent of sex, body size, or reproductive stress. Second, there were no differences in the prevalence of ticks or chiggers or in the intensity of tick parasitism among the different age and sex classes within bands, including adult females and subadult males. Because males leave their natal social groups after their testes descend (that is, sexual maturity is reached while males are still band members) and after they are larger than adult females, differences in ectoparasitism as a result of sex must commence after males become solitary, irrespective of the onset of maturity. Therefore, male adulthood alone does not explain the increased parasitism by ticks. Third, in 8 of 9 examined months (Table 3), prevalence of chiggers on males was < 50%. The exception was January 1995 when prevalence was 100% ( $n = 4$ ). Based on data from trapped males, high prevalence was also found in January 1992 (75%;  $n = 4$ ). January marks the start of the brief mating season when

males attempt to join bands for several weeks to mate with females. Fruit is also rare in January and solitary males and band members are often observed simultaneously feeding at the same food resource (Gompper, 1996). Thus, although the sample sizes are small, the finding of increased chigger prevalence among solitary males in January supports the importance of social structure rather than host sex in explaining the patterns of parasitism.

A temporal perspective was important in relating variation in parasite prevalence (ticks and chiggers) and intensity (ticks) to host social structure. Differences in tick intensities among solitary and social individuals would not have been identified if only data from the dry season were analyzed, even though tick intensities in the dry season were much higher than in the wet season. However, host social structure also was important for identifying temporal changes, or lack thereof, in parasite burden. Data collected over a long period but without information on social structure might not have revealed that chigger prevalence within social groups fluctuates independently and greatly over short periods of time, and that this pattern does not occur within the population of solitary adult males.

Increased chigger prevalence on band members was unexpected, and cannot be explained by the increased contact rates of band members since chiggers are not transmitted between individuals. It is possible that the ranging patterns of band members result in greater opportunity for contact with chiggers compared to solitary adult males. Previous work, however, has shown that solitary males and bands have home ranges that are equal in size and overlap extensively and that solitary males and band members use the same resources, such as fruiting trees, during the same time periods (Gompper, 1996, 1997). It is also possible that living in close association with conspecifics creates a larger CO<sub>2</sub> plume than that produced by a solitary individual. Chiggers would be attracted to the plume created by a band from a larger area and for a longer period, and would be more likely to encounter a potential host. Presumably this CO<sub>2</sub> plume, as well as similar cues such as host odor, would also attract greater numbers of ticks. Individual band members would, however, benefit in avoiding parasitism by ticks by allogrooming.

Significant differences between tick intensities on solitary males and band members were observed

only during the wet season when populations of ticks are smaller, and not during the dry season when populations are larger. This unexpected finding may be an artifact of the smaller sample size of coatis trapped during the dry season. Alternatively the result is real, which is supported by the observation that the prevalence of ticks on band members also increases to a quantity approximately equal to that found among males during both wet and dry seasons (Table 2). This suggests that during the dry season allogrooming may be insufficient to reduce tick prevalence or intensities to a quantity lower than that found among solitary individuals.

Finally, these results show that the dynamics of ectoparasite infrapopulations (all individuals of a species on an individual host at a particular time; Bush et al., 1997) depend on the extent of host sociality. This in turn implies that the ectoparasite component community (sensu Bush et al., 1997) may also differ for subsets of hosts such as group-living and solitary coatis. Generalizing the importance of host sociality will be difficult, however, as ectoparasite prevalence is influenced by many factors, including parasite size and host seeking behavior.

## Acknowledgments

I thank J. Berger, C. Elphick, A. Hoyleman, R. List, R. Medellín, J. Rachlow, and an anonymous reviewer for comments and assistance. William Wrenn confirmed the chigger identity. Financial support came from the National Science Foundation (DEB 9212747), Smithsonian Institution, Fulbright Foundation, Sigma Xi, Explorers Club, American Museum of Natural History, American Society of Mammalogists, and the University of Tennessee.

## Literature Cited

- AESCHLIMANN, A. 1991. Ticks and disease: susceptible hosts, reservoir hosts, and vectors. Pp. 148-156 in *Parasite-host associations* (C. A. Toft, A. Aeschlimann, and L. Bolis, eds.). Oxford University Press, 384 pp.
- ALEXANDER, R.D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics*, 5:325-383.
- BRENNAN, J.M. AND C.E. YUNKER. 1966. The chiggers of Panama (Acarina: Trombiculidae). Pp. 221-266 in *Ectoparasites of Panama* (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, 861 pp.
- BUSH, A.O., K.D. LAFFERTY, J.M. LOTZ, AND A.W. SHOSTAK. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology*, 83:575-583.
- CÔTÉ, I.M. AND M.R. GROSS. 1993. Reduced disease in offspring: a benefit of coloniality in sunfish. *Behavioral Ecology and Sociobiology*, 33:269-274.
- CÔTÉ, I.M. AND R. POULIN. 1995. Parasitism and group size in social animals: a meta-analysis. *Behavioral Ecology*, 6:159-165.
- DAVIES, C.R., J.M. AYRES, C. DYE, AND L.M. DEANE. 1991. Malaria infection rate of Amazonian primates increases with body weight and group size. *Functional Ecology*, 5:655-662.
- FAIRCHILD, G.B., G.M. KOHLS, AND V.J. TIPTON. 1966. The ticks of Panama (Acarina: Ixodoidea). Pp. 167-219 in *Ectoparasites of Panama* (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, 861 pp.
- FREELAND, W.J. 1977. Blood-sucking flies and primate polyspecific associations. *Nature*, 269:801-802.
- \_\_\_\_\_. 1979. Primate social groups as biological islands. *Ecology*, 60:719-728.
- GOMPPER, M. E. 1996. Foraging costs and benefits of coati (*Nasua narica*) sociality and asociality. *Behavioral Ecology*, 7:254-263.
- \_\_\_\_\_. 1997. Population ecology of the white-nosed coati (*Nasua narica*) on Barro Colorado Island, Panama. *Journal of Zoology*, London, 241:441-455.
- GOMPPER, M.E., J.L. GITTLEMAN, AND R.K. WAYNE. 1997. Genetic relatedness, coalitions and social behavior of white-nosed coatis, *Nasua narica*. *Animal Behaviour*, 53:781-797.
- HOCHBERG, M. E. 1991. Viruses as costs to gregarious feeding behaviour in the Lepidoptera. *Oikos*, 61:291-296.
- KAUFMANN, J. H. 1962. Ecology and the social behavior of the coati, *Nasua narica*, on Barro Colorado Island, Panama. University of California Publications in Zoology, 60:95-222.
- KEYMER, A.E. AND A.F. READ. 1991. Behavioural ecology: the impact of parasitism. Pp 37-61 in *Parasite-host associations* (C. A. Toft, A. Aeschlimann, and L. Bolis, eds.). Oxford University Press, 384 pp.
- LEVIN, M.L. AND D. FISH. 1998. Density-dependent factors regulating feeding success of *Ixodes scapularis* larvae (Acari: Ixodidae). *Journal of Parasitology*, 84: 36-43.
- MØLLER, A.P., R. DUFVA, AND K. ALLANDER. 1993. Parasites and the evolution of host social behavior. *Advances in the Study of Behavior*, 22:65-102.
- MOORING, M.S. AND B.L. HART. 1992. Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. *Behaviour*, 123:173-193.
- NOBLE, E.R., G.A. NOBLE, G.A. SCHAD, AND A.J. MACINNES. 1989. Parasitology. The biology of animal parasites. Sixth edition. Lea and Febiger, Philadelphia, 574 pp.
- PORTEOUS, I.S. AND S.J. PANKHURST. 1998. Social structure of the mara (*Dolichotis patagonum*) as a determinant of gastrointestinal parasitism. *Parasitology*, 116:269-275.
- RUBENSTEIN, D.I. AND M.E. HOHMANN. 1989. Parasites and social behavior of island feral horses. *Oikos*, 55:312-320.
- SASA, M. 1961. Biology of chiggers. *Annual Review of Entomology*, 61:221-244.

WALADDE, S. M. AND M. J. RICE. 1982. The sensory basis of tick feeding behavior. Pp 71-118 *in* Physiology of ticks (F. D. Obenchain and R. Galus eds.). Pergamon Press, Oxford, 509 pp.

WRIGHT, S. J., M. E. GOMPPER, AND B. DELEON. 1994. Are large predators keystone species in Neotropical forests? The evidence from Barro Colorado Island. *Oikos*, 71:279-294.