SOCIAL STRUCTURE OF FERAL HORSES IN THE LLANOS OF VENEZUELA

M. ANDREÍNA PACHECO AND EMILIO A. HERRERA

Departamento de Estudios Ambientales, Universidad Simón Bolívar, Apartado 89.000, Caracas 1080-A, Venezuela

Feral horses (*Equus caballus*) in the Venezuelan savannas (llanos) formed bands of 3–35 individuals; mean group size varied between 15 and 21. Some bands had up to three adult males, and there was a positive correlation between the number of males and the number of females in bands. Adult males also were seen solitary or formed bachelor groups. One association of three females was observed for 3 months. We noted a correlation between number of females in bands and number of foals per female born during our study (January–July 1992). The advantages of being in larger groups were unclear, because natural predators were rare. Perhaps females in larger groups have more time available for foraging due to reduced individual vigilance or that larger groups live in better-quality home ranges.

Key words: *Equus caballus*, feral horses, social structure, llanos, Venezuela

Species of the genus *Equus* exhibit two main types of social organization; permanent groups and temporary associations. Klingel (1974) noted that temporary associations are typical of *E. africanus*, *E. hemionus*, and *E. grevyi*. This type of nonpermanent association includes animals of one or both sexes. *E. przewalski*, *E. caballus*, *E. burchelli*, and *E. zebra* form permanent groups called bands, which are composed of one adult male (sometimes more than one) and his harem. The harem includes the females and their offspring (infants and juveniles). Adult males without a harem occur solitarily or in bachelor groups (Klingel, 1974). From his studies of the socioecology of equids, Rubenstein (1986) concluded that the abundance, quality, and distribution of resources were important factors determining the types of association, and patterns of distribution and activity of female feral horses. In general, where resources were abundant and evenly spread, females formed permanent associations; where resources were less abundant and more patchy, groups were smaller and ephemeral. Under either of these scenarios, the reproductive success of a male depended on his ability to attract a large number of females and to maintain his harem (Rubenstein, 1986, 1989). Berger (1988), however, using mostly experimental evidence, emphasized the potential relevance of phylogeny playing a role in these patterns, but acknowledged that many experiments could not distinguish between adaptation and phylogenetic inertia.

Most studies of feral or wild horses have been conducted in temperate zones, particularly in the deserts and mountains of northwestern North America (Berger, 1977; Bowling, 1994; Miller and Denniston, 1979), on islands off the Atlantic Coast (Berger, 1986; Franke Stevens, 1989; Kirkpatrick and Turner, 1991; Rubenstein, 1981), and in southern France (Duncan, 1980; Feh, 1990). In these areas, wild horses mate in spring, when grass becomes abundant, and females give birth to a single young 11 months later. Therefore, females can only reproduce once per year (Berger, 1977). Once juveniles of both sexes reach sexual maturity, they typically abandon their parental band. Females quickly find and enter other bands, whereas most males form permanent bachelor groups or become solitary (Berger, 1987).

Horses were introduced into South America by the European colonizers in the 16th century. Many feral populations were founded and today feral horses occur in Argentina, Brazil, Chile, Peru, and Venezuela (Berger, 1986). In Venezuela, no studies on the behavior or ecology of feral horses have been conducted and little is known of feral horses in tropical areas in general. For this reason, the main objective of our study was to describe the social structure of feral horses in the Venezuelan savannas (llanos), and to compare it with the social structure described for feral horses in temperate zones. To achieve this, we studied size and composition of groups, the general behavior of individuals within groups, and the seasonal changes in these variables, in the region known as the llanos of Venezuela. We also studied some aspects of reproduction in these animals. In particular, we examined seasonality of mating behavior and births of young, and tested whether size of group had an effect on the reproductive success of females.

Materials and Methods

This study was conducted at Hato El Frío (7°46′N, 68°57′W), an 80,000-ha cattle ranch located in the Venezuelan savannas (llanos) that are flooded seasonally. The region is characterized by vast expanses of flat grassland interspersed with isolated patches of woodland. Despite the homogeneous appearance of the habitat, there are three physiographic units termed banco, bajío and estero, differing in their relative height, soil type, and vegetation cover. Bancos constitute the highest ground (≤2 m above the lowest points) and are covered by tall grasses (e.g., *Imperata contracta*) or bushes (e.g., *Sida*, *Hyptis suaveolens*). Bajíos are intermediate in height, account for ca. 75% of the area, and are covered with short grasses such as *Leersia hexandra* and *Panicum laxum* (Ramia, 1972). In the wet season, bajíos can be flooded to ca. 20-cm deep. Esteros are ponds of varying size where a number of species of aquatic grasses (*Hymenachne amplexicaulis*) and other plants grow. Esteros typically dry up in the dry season.

The major climatic feature of the llanos is the alternation of wet (May–October) and dry (November–April) seasons. During the wet season extensive flooding occurs, whereas in the dry season most esteros dry up leading to severe scarcity of water in February and March. To have water available for cattle during the dry season, dams (2-m high by 3 km long) have been built at El Frío, causing some relatively large areas to be flooded deeper than usual (Ramia, 1972).

El Frío contains a central area of 10,000–15,000 ha that is considered a wildlife reserve and where feral horses are common. About 1,500 animals live there (Anonymous, 1988). The population of feral horses of El Frío has lived free from human intervention for many generations except for one factor; every year 250–300 young animals are captured and taken as work animals (Anonymous, 1988). Cowboys preferentially take males from what appear to be bachelor groups.

We regularly censused groups of feral horses and made observations on the general behavior of individuals in these groups. We selected a 20-km route that could be accessed year-round in a four-wheel-drive vehicle. We censused the route for 4–5 days each month from 0800 to 1800 h from January to July 1992 (ca. one-half the dry and one-half the wet seasons). We stopped systematically every 1 km, to search for horses in a full circle around each location, and recorded all types of associations observed. Animals were observed from inside or from the top of the vehicle using 8 by 40× binoculars and a 15–60× spotting scope.

For each association of horses we recorded the number of individuals in each age class, noting sexes when possible. Animals born during the study period were considered foals (1–6 months old). Other young animals were distinguished from adults by their smaller body and shorter length of mane, and were recorded as juveniles. Each individual was described according to its color pattern, length of mane, and length of tail, making many of them individually identifiable (Berger, 1977; Feist and McCullough, 1976; Franke Stevens, 1990; Rubenstein, 1986; Turner et al., 1981).

We were able to identify some groups for several consecutive months, and we assigned them names in relation to the area where they were seen. We made further observations on these groups, in sessions lasting ≤2 h, recording all

behavioral events observed (Martin and Bateson, 1986).

Results

We identified the following types of association among feral horses at Hato El Frío. A band was a group formed by one or more adult males (up to three), with several females and their young. Bachelor groups contained males, but no females or young. Solitary males also were recorded, as well as groups of females without males or young.

In May, June, and July all individuals were seen in bands, whereas in the other months 2–4% were seen in other types of associations. Horses usually occurred around streams and large ponds, where green grass was abundant. Bands varied widely in size; the two smallest bands were formed by three adults (one male and two females) and one young, whereas the largest had 35 individuals; 3 adult and 3 juvenile males, 22 females, and 7 young. Monthly mean ($\bar{X} \pm SD$) size of bands (Fig. 1) varied between 15.5 ± 7.3 and 20.8 ± 7.3. Size of bands slightly increased from February through May, when most foals were born, and decreased in June and July (Fig. 1).

We noted a significant positive correlation between number of females and number of males in bands (Spearman-rank correlation coefficient, $r_s = 0.871$, $n = 8$, $P < 0.05$). This analysis was performed for data collected on eight bands for which adequate data were available and in July, (i.e., after the period when young males leave harems), to avoid nonpermanent members of the group affecting this correlation.

Monthly sex ratio (males : females) in all bands varied between 1:3.3 and 1:4.7. The overall sex ratio in the population for each month sampled ranged between 1:3.0 and 1:5.2. From January through March 1992, a single all-female group was identified, formed by three adults (≤2 years old). This was the only all-female group that we recorded and it disappeared after April. Four

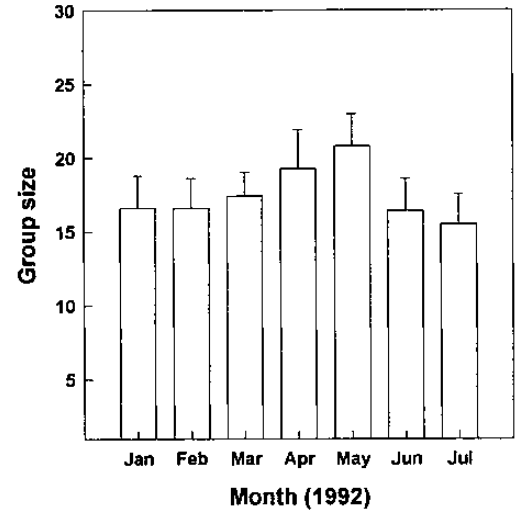

FIG. 1.—Means (±1 *SD*) of number of individuals from all age-classes in bands of feral horses at Hato El Frío, Venezuela, January–July 1992.

bachelor groups were observed, two of which had two members, one had three, and another had eight individuals. These groups were observed January through April, but only the group of three males was recorded on 2 consecutive months (February and March). Bachelor groups and the group of females generally were seen close to areas where bands occurred. We also recorded two solitary males. Both individuals were observed around small lagoons together with cattle. These males were rather small with short manes and tails, indicating that they were young adults.

Detailed behavioral observations were conducted for only two bands, Manirito and Chupadero, both of which regularly were observed for several consecutive months. The monthly number of individuals in band Manirito ranged between 31 and 35. This group initially contained six males; three adults and three juveniles. After February, nine females and two males left the group. Also, by the end of the study period 10 births had occurred, of which six were females and four were males. These events accounted for the major changes in size and

composition of groups. Of the three adult males in this band, only one was seen to mount two females in April, whereas the other two males disappeared from the group in June.

The band at Chupadero could only be observed from February to June. This band had 22–30 individuals and also experienced variation in group composition, mostly owing to females entering or leaving the group: in March, one female left; in April, seven females came into the group; by May, five females had disappeared. One juvenile male (there were three adult and three juvenile males) abandoned the group in May while a different one entered the band that same month. A total of seven births were recorded in this band during the study period. Two of the three adult males in this band were seen copulating with two different females.

During a total of 152 h of observation on these two bands (of 279 h overall observation), we observed no aggressive interactions among their members. We did record, on two occasions, one of the adult males of the band at Chupadero facing a group of three males, and chasing them from his group's area. This was not one of the males previously seen mating.

Because natural predators (i.e., large cats) are nearly extinct in the study area, we never observed attacks on the horses. On 14 occasions however, when a band was frightened (mostly by men on horseback), the band ran away with the only male, first "pushing" the band from behind and then moving to the front to lead it. On nine occasions, when more than one male was present, the male who appeared to be dominant led the fleeing group, whereas another male apparently "helped" by remaining at the back, perhaps contributing to the group's cohesion during flight.

For four bands, we were able to tally the number of foals born each month that survived to the following month. Twenty-four young were born during our study period, most of them in the dry season; February (10 young), March (4 young) and April (5 young). The proportion of young in bands increased from 0.009 (n = 104 individuals of all ages) in January to 0.15 (n = 139)–0.16 (n = 163) in March and April, respectively, and to 0.21 (n = 108)–0.26 (n = 66) by the end of the study period. The sex ratio in foals was 1:1.

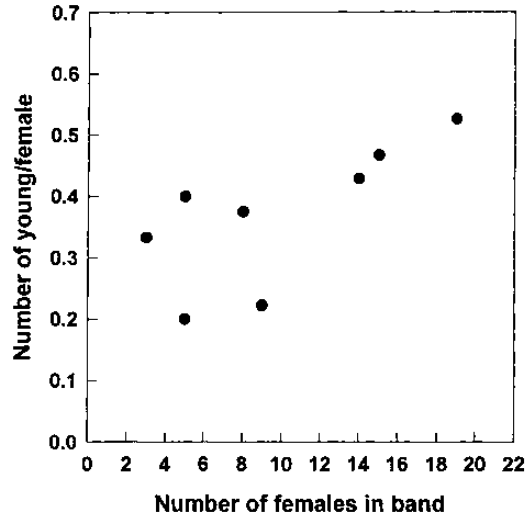

FIG. 2.—Proportion of young per female for eight well-known bands of feral horses at Hato El Frío, Venezuela. Young were born during January–July 1992.

Figure 2 shows that the number of foals per female increases with the number of females in the bands (r_2 = 0.743, n = 8, P < 0.05). Because mares have only one foal, this correlation indicates that a greater number of females bred in larger bands that in smaller ones. Between March and May, we observed 13 matings, 11 of these in April, coinciding with the beginning of the rains.

DISCUSSION

At Hato El Frío, we observed the three basic social units described for feral horses by previous authors (Berger, 1977; Feist and McCullough, 1976; Klingel, 1974; Miller and Denniston, 1979; Rubenstein, 1981; Wells and Von Goldschmidt-Rothschild, 1979); bands, bachelor groups, and solitary males. Bands generally were stable in size

and composition with the exception of the band at Chupadero, from which several females left, while others joined, during the study. Bachelor groups were composed of two or three individuals, except one that was formed by eight males, in accordance with the previous findings by Feist and McCullough (1976) and Berger (1977). We also observed what appears to be a previously undescribed association, i.e., a group of just three adult females (although ephemeral all-female groups have been reported—Berger, 1986). This may be related to the female-biased sex-ratio, which in turn may be caused by the annual extraction of predominantly male horses that cowboys remove every year.

One important difference between the population from El Frío and populations from temperate zones was that bands were larger at El Frío. Bands with 15–20 adults were common in our study area, whereas in temperate zones bands usually have three to eight adults (Berger, 1977, 1983; Feh, 1990; Feist and McCullough, 1976; Franke Stevens, 1989; Miller, 1981). Only Miller and Denniston (1979) reported groups of 2–16 individuals, with a single instance of 20 individuals, in Sweetwater Co., Wyoming.

The larger size of bands we observed may be related to a number of factors. First, dry and rainy seasons in the tropical climate of the Venezuelan llanos are different from the four seasons of temperate zones. As we have mentioned, horses usually were observed around free water. During the dry season, esteros (shallow marshes or ponds) dwindled, causing groups of horses to aggregate around them where grass was abundant. In wet months, the llanos were extensively flooded, leaving only isolated patches of higher ground (bancos), where several bands grouped together with cattle. Therefore, in both seasons, either because of the scarcity of water or because of flooding, bands were forced to be close to each other. Thus, transfers of individuals between bands may occur as reported by Rutberg (1990), and there is opportunity for males to compete for a greater number of females in their bands (Berger, 1986). Both of these processes could lead to larger bands. As previous authors have reported, when resources are homogeneously distributed, dominant males of groups fight other males to increase the size of their harems and thereby their reproductive success (Berger, 1987; Feist and McCullough, 1976; Rubenstein, 1981).

Larger size of bands also may have been favored by the presence of more than one adult male. Groups with 21–35 individuals had two to three adult males and those with <21 generally had only one (Fig. 2). Although the presence of more than one male in bands is not a prerequisite for a larger band, it may play a role in the stability of large groups (Franke Stevens, 1990), because males could collaborate in the care of females and young in the group. Although living in a larger group may be beneficial to all group members, the additional males would obtain the advantage of mating opportunities. For the dominant male, the loss in matings to other males in his band may be compensated by the extra females with which he also could copulate. We have evidence of at least one instance in which more than one male mated in the multimale bands. Miller and Denniston (1979), Miller (1981), Franke Stevens (1989, 1990) and Eagle et al. (1993), all reported bands with more than one male. These authors suggested that bands with two adult males are larger and more stable because there is a hierarchy among the males, and subordinate males did not allow females to disperse and abandon the group. In our study, we noted evidence of collaboration by the apparently subordinate male while bands were fleeing.

Franke Stevens (1990) reported that, in the islands of North Carolina, the dominant male in bands with more than one male is the only one to mate. Miller (1981) conversely, described a linear hierarchy among males in multi-male bands, and reported that $\leq 42\%$ of the matings were performed

by subordinate males, whereas dominants obtained 49% (the remaining 9% was performed by outside males). Miller (1981) also described three mating systems in multi-male bands: all males in the band may mate with the same female; each male associates with one female, with which he mates and watches to prevent other males from mating with her; the dominant male performs most of the mountings. In the Red Desert, Miller (1981) could not determine which form was more common, but the system seemed to change with time and across bands.

Although we were unable to detect a hierarchy among males, we did record more than one male mating in one of our study bands. The only possible evidence in favor of the existence of dominance relationships in our bands was that only one of the males led when fleeing while the others appeared to help. Miller (1981) reported that subordinate males were more active in interband aggression, which is consistent with our observation of a male, apparently not the dominant, which chased three foreign males from the area of his band.

The slight increase in size of band from January through May (Fig. 1) was mostly due to the number of foals born during this period. In June and July, however, we observed a decrease in mean size of groups, apparently because of juveniles leaving bands in the mating period. Berger (1986) reported that young horses in the Great Basin leave their natal bands voluntarily, but in the llanos, the nature of this process is unknown. The possible factors promoting dispersal of juveniles appear to be inbreeding avoidance (Feist and McCullough, 1976), reproductive competition between parents and offspring, and competition for resources between juveniles and adults (Duncan et al., 1984).

The sex ratio (males females) among adults in our study population (1:3–4) was more biased toward females than that reported in previous studies (1:2 in Berger, 1986), whereas that of young was unbiased (1:1) in accordance with previous reports (Garrott, 1991). The greater proportion of females in our study may be related to the cowboys removing more males than females from the population of feral horses. Many of the animals captured this way are young males from bachelor groups. This may be the reason that most animals were seen in bands, and could be the factor underlying the similarity of sex ratios for bands and for the population as a whole. Further, the relative scarcity of males may be related to the larger size of bands (compared with temperate regions), although this would appear to be incompatible with the observation that some bands had more than one male.

During our study, the greatest number of matings occurred at the beginning of the rainy season (April), possibly in relation to the increase in availability of grass at this time. Working back from the peak of births (February) in 1992, we infer that the previous peak of matings occurred in March 1991 (11 months earlier). This coincides with the beginning of rains that year, which started 1 month earlier than usual (March rather than April). In temperate zones, the period of mating and births occurs during spring, proximately triggered by photoperiod (e.g., Rossdale and Ricketts, 1980), and ultimately is related to abundance of resources (Berger, 1987; Feist and McCullough, 1976; Seal and Plotka, 1983). In the llanos, however, births occur in the dry season (January–March), a time of scarce resources. This may be disadvantageous, albeit for a short period, for the female as well as for her newborn, because she will have to graze on the dry and less-nutritious grass of the dry season while lactating. Shortly thereafter the rains usually start.

A greater proportion of females from larger groups had young than those from smaller bands (Fig. 2). There are at least two possible advantages to living in a large group. One is that animals in larger groups would have to spend less time being vigilant (Elgar, 1989; Yaber and Herrera, 1994).

Although actual predators are rare, bands of feral horses often are disturbed by humans and other factors. If vigilant animals reduce the amount of daily disturbance, females would have a greater proportion of their time available for grazing during gestation and lactation. Secondly, larger groups may live in better-quality home ranges. Although we have no evidence of territoriality among our bands, there are reports of intergroup aggression in other areas (Miller and Denniston, 1979; Rubenstein, 1981). Larger groups may be favored in these conflicts, as Miller and Denniston (1979) reported, enabling these bands to secure larger home ranges or home ranges located in better habitat.

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Literature Cited

Anonymous. 1988. Hato El Frío: enorme reservorio del caballo llanero. Venezuela Bovina, 3:43–48.

Berger, J. 1977. Organizational systems and dominance in feral horses in the Grand Canyon. Behavioral Ecology and Sociobiology, 2:131–146.

———. 1983. Predation, sex ratios and male competition in equids (Mammalia: Perissodactyla). Journal of Zoology (London), 210:205–206.

———. 1986. Wild horses of the Great Basin: social competition and population size. The University of Chicago Press, Chicago, 326 pp.

———. 1987. Reproductive fate of dispersers in a harem-dwelling ungulate: the wild horse. Pp. 41–54, *in* Mammalian dispersal patterns (B. D. Chepko-Sade and Z. T. Halpin, eds.). The University of Chicago Press, Chicago, 342 pp.

———. 1988. Social systems, resources and phylogenetic inertia: an experimental test and its limitations. Pp. 157–186, *in* The ecology of social behavior (C. N. Slobodchikoff, ed.). Academic Press, San Diego, California, 429 pp.

Bowling, A. T. 1994. Population genetics of Great Basin feral horses. Animal Genetics, 25(Supplement 1):67–74.

Duncan, P. 1980. Time budgets of Camargue horses. II. Time budgets of adult horses and weaned subadults. Behaviour, 71:26–49.

Duncan, P., C. Feh, J. C. Gleize, P. Malkas, and A. M. Scott. 1984. Reduction of inbreeding in a natural herd of horses. Animal Behaviour, 32:520–527.

Eagle, T. C., S. A. Cheryl, R. A. Garrott, E. D. Plotka, D. B. Siniff, and J. R. Tester. 1993. Efficacy of dominant male sterilization to reduce reproduction in feral horses. Wildlife Society Bulletin, 21:116–121.

Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirircal evidence. Biological Review, 64:13–33.

Feh, C. 1990. Long-term paternity data in relation to different aspects of rank for Camargue stallions, *Equus caballus*. Animal Behaviour, 40:995–996.

Feist, J. D., and D. R. McCullough. 1976. Behavior patterns and communication in feral horses. Zeitschrift für Tierpsychologie, 41:337–371.

Franke Stevens, E. 1989. Contests between bands of feral horses for access to fresh water: the residents win. Animal Behaviour, 40:995–996.

———. 1990. Instability of harems of feral horses in relation to season and presence of subordinate stallions. Behaviour, 112:149–159.

Garrott, R. A. 1991. Sex ratios and differential survival of feral horses. The Journal of Animal Ecology, 60:929–937.

Kirkpatrick, J. F., and J. W. Turner. 1991. Changes in herd stallions among feral horse bands and the absence of forced copulation and induced abortion. Behavioral Ecology and Sociobiology, 29:217–219.

Klingel, H. 1974. A comparison of the social behavior of the Equidae. Pp. 124–132, *in* The behavior of ungulates and its relation to management (V. Geist and F. Walther, eds.). International Union for the Conservation of Nature and Natural Resources Publications New Series, Morges, Switzerland, 24:1–511.

Martin, P., and P. Bateron. 1986. Measuring behavior: an introductory guide. Cambridge University Press, Cambridge, United Kingdom, 200 pp.

Miller, R. 1981. Male aggression, dominance and breeding behavior in Red Desert feral horses. Zeitschrift für Tierpsychologie, 57:340–351.

Miller, R., and R. H. Denniston. 1979. Interband dominance in feral horses. Zeitschrift für Tierpsychologie, 51:41–47.

Ramia, M. 1972. Cambios en la vegetación de las sabanas del hato El Frío causados por diques. Boletín de la Sociedad Venezolana de Ciencias Naturales, 30:57–90.

Rossdale, P. D., and S. W. Ricketts. 1980. Equine stud farm medicine. Second ed. Baillière Tindall, London, United Kingdom, 564 pp.

Rubenstein, D. I. 1981. Behavioral ecology of island feral horses. Equine Veterinary Journal, 13:27–34.

———. 1986. Ecology and sociality in feral horses and zebras. Pp. 282–301, *in* Ecological aspects of

social evolution (D.I. RUBENSTEIN and R. WRANGHAM, eds.). Princeton University Press, Princeton, New Jersey, 551 pp.

———. 1989. Life history and social organization in arid adapted ungulates. Journal of Arid Environments, 17:145–156.

RUTBERG, A. T. 1990. Inter-group transfer in Assateague pony mares. Animal Behaviour, 40:945–952.

SEAL, U. S., AND E. D. PLOTKA. 1983. Age-specific pregnancy rates in feral horses. The Journal of Wildlife Management, 47:422–429.

TURNER, J. W., A. PERKINS, AND J. F. KIRKPATRICK. 1981. Elimination marking behavior in feral horses. Canadian Journal of Zoology, 59:1561–1566.

WELLS, S. M., AND B. VON GOLDSCHMIDT-ROTHSCHILD. 1979. Social behavior and relationships in a herd of Camargue horses. Zeitschrift für Tierpsychologie, 49:363–380.

YABER, M. C., AND E. A. HERRERA. 1994. Vigilance, group size and social status in capybaras. Animal Behaviour, 48:1301–1307.

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