



Parasites and Social Behavior of Island Feral Horses

Daniel I. Rubenstein; Marlies E. Hohmann

Oikos, Vol. 55, No. 3. (Jul., 1989), pp. 312-320.

Stable URL:

<http://links.jstor.org/sici?sici=0030-1299%28198907%2955%3A3%3C312%3APASBOI%3E2.0.CO%3B2-9>

Oikos is currently published by Nordic Society Oikos.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/oikos.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

Parasites and social behavior of island feral horses

Daniel I. Rubenstein and Marlies E. Hohmann

Rubenstein, D. I. and Hohmann, M. E. 1989. Parasites and social behavior of island feral horses. – *Oikos* 55: 312–320.

The horses of Shackelford Banks, North Carolina, USA, are heavily parasitized by intestinal worms and harassed by dipterans, and although both types influence behavior only internal parasites affect bodily condition and the structuring of horse society. Thirteen species of internal parasites were identified, but only 4 of 13 groups contain them all and even within groups differences among individuals are large. Among individuals ova emissions vary ranging from 50 to 76,875 eggs per gram. The most important environmental factors influencing egg production are season and a group's location on the island, presumably because of salinity and soil differences and their effects on ova survival. Of the social and life history factors, age, and group size, but neither reproductive state nor dominance status are important. The fitness consequences of internal parasitism may be large since the number emitted is negatively correlated with next year's bodily condition. Biting fly burdens are also affected by a variety of environmental factors. In general, horses are covered with more flies on sunny days, when winds are moderately brisk, when occupying dunes, and around mid-day. In contrast to endoparasites, fly burden is affected by reproductive condition and dominance status and tends to decrease as groups increase in size. Since groups do not grow very large, nor do females attempt to bring groups together, the negative effects of endoparasites appear to override those associated with ectoparasites. Consequently, endoparasites appear to exert a stronger influence on social structure, even though ectoparasites seem to play a stronger role in shaping details of behavior.

D. I. Rubenstein and M. E. Hohmann, Biology Dept, Princeton Univ., Princeton, NJ 08544, USA.

Introduction

Internal and external parasites can have severe, often debilitating, effects on the health and reproductive success of mammals in the wild (Talbot and Talbot 1963, Halvorsen 1986). While migrating as larvae, internal parasites, especially intestinal ones, can damage tissue and, when sedentary as adults, can cause anemia and the usurpation of a host's nutrients and vitamins. And in addition to spreading disease, biting flies often cause the loss of large quantities of blood (Tashiro and Schwardt 1953), time to be wasted on comfort movements, or feeding opportunities to be lost when movements to refuges are necessary. Moreover, for social animals the likelihood of parasite and disease transmission is thought to automatically increase by living in groups (Alexander 1974, Hoogland 1979, Brown 1985),

with the effects often being felt unequally by individuals of different social status (Christian and Davis 1964, Hausfater and Watson 1976, Holmes 1982, Halvorsen 1986).

To some extent social animals are able to limit these debilitating effects. Horses, bison and caribou typically rest in open areas, on windswept ridges, or even in shallow bodies of water to escape swarms of biting flies, mosquitoes and other insect pests (Berger 1986, Espmark and Langvatn 1979, Duncan and Cowtan 1980, Keiper and Berger 1982). Monkeys in African forests often form large multispecies groups at times of the day when biting flies are most active (Freeland 1977). This serves to reduce an individual's level of harassment, a benefit that also accrues to horses living in large groups (Duncan and Vigne 1979). And although social grooming among primates and ungulates acts to cement many

Accepted 16 January 1989

© OIKOS

types of social relationships, it serves, and probably evolved, to facilitate the removal of ectoparasites (Seyfarth 1983, Hausfater 1985). Even the ingestion of endoparasites by ungulates can be reduced by grazing in areas far from those used repeatedly by the group for defecating (Miller 1953).

Clearly, social animals can modify their behavior to reduce the effects of parasites. Yet no systematic study has examined the overall effects of both internal and external parasite loads on social organization. The purpose of this study is first to determine what social and environmental factors facing a population of feral horses are associated with the high rates of intestinal ova emission and high levels of harassment by biting flies, and second to measure the effect of different levels of infection on the structure of horse society.

Materials and methods

During 1984 the population of feral horses inhabiting Shackleford Banks, a barrier island off the coast of North Carolina, USA, reached 92. There horses either live in one of 16 harems, each consisting of a group of unrelated adult females, their juvenile offspring, and a single male, or in one of the few all male 'bachelor' groups. Although the island is 17 km long and never more than 2.5 km wide, horses only reside near the ends. Thus two sub-populations, each consisting of 8 harems, rarely come into contact. Those near the western end of the island display the typical pattern of extensive overlap among group ranges, but those near the eastern end are socially more diverse. Two-thirds of the harems, those situated in the far east, live in small exclusive territories that are defended solely by stallions, whereas the rest, those inhabiting the middle-eastern part of the island occupy ranges that overlap (Rubenstein 1981, 1986).

The island is vegetated by three grass communities which run along the long axis of the island. On the eastern end a salt marsh dominated by *Spartina alterniflora* and *Salicornia* spp. borders the back sound, whereas a row of low dunes covered with *Uniola paniculata* protects the island from the surf. In between is a swale composed primarily of *Spartina patens* and *Muhlenbergia* spp. that is occasionally punctuated by small stands of maritime forest. On the western end swale is limited to patches among a continuous range of tall dunes, dense forest, and pockets of freshwater marsh. The only extensive salt marsh on the west is restricted to the island's tip. These different vegetational arrangements account for the regional differences in social organization (Rubenstein 1981, 1986), and each vegetation zone must be grazed regularly to maintain bodily condition, although usage varies by season (Rubenstein 1981).

Sixty-one horses were examined for endo- and ectoparasitic infection from June through July and again in November 1984. Fresh dung samples were collected and

placed in zip lock bags and cooled in ice until they could be transported to the mainland. There samples were either cultured for nematode larvae or refrigerated until nematode eggs could be counted. Eggs of *Anoplocephala magna*, *A. perforata*, *Parascaris equorum*, *Strongyloides westeri*, *Dictyocaulus arnfieldi*, *Fasciola hepatica*, and *Oxyuris equi* could be microscopically identified to species, but those of the strongyles could not. Eggs were counted using a variation of the McMaster technique (Levine et al. 1980). First, two grams of feces were mixed with 8 ml of saturated NaCl solution. Then test tubes were centrifuged for three minutes at 1500 rev min⁻¹ to separate debris. Finally two microliters of the mixed suspension were transferred to Neubauer 0.1 mm deep 2 chambered Hemacytometers. Egg counts by species from at least 8 chambers were used to compute average number of eggs produced per gram (epg). Cultures of infective third stage larvae were established following the technique of Dunn (1978) to separate the strongyle eggs into species. A sample of 100 were then identified to determine the identity and proportion of each of the following species: *Strongylus vulgaris*, *S. edentatus*, *S. equinus*, *Cylicocercus goldi*, *C. catinatus*, *Cylicodontophorus bicoronatus*, *C. ultrajectinus*, *Poteriostomum* spp., *Gyalocephalus* spp., *Trichostrongylus axei*, and *Strongyloides westeri*.

Dipterans that bite horses were counted by scanning horses with binoculars from a distance of 5–10 meters. Green headed horseflies, *Tabanus nigrovittatus* and *T. lineola*, deer flies *Chrysops fuliginosus* and *C. atlanticus*, as well as stableflies *Stomoxys colcitrans* were large enough to count individually, but mosquitoes were not. Individual horses were followed for several hours and the number of flies settled on, or hovering over, the body were counted every 10 min. Horses typically try to rid themselves of flies by twitching muscles, swishing tails, shaking manes or stamping, kicking, biting, nuzzling or rolling. Any such comfort movements made during one minute after a fly count were tallied and used to estimate fly attack rate and provided a relative measure of how seriously horses were being harassed by biting flies. The replicate counts of fly abundances and comfort movements for each individual during a given follow were then averaged.

After each fly count the following series of environmental and social variables were also recorded: location (East, Mid-east, or West), vegetation zone (Marsh, Swale or Dune), wind velocity (Beaufort scale 0–12), sky condition (Clear, Overcast, or Partly overcast), as well as the number of horses in both its harem and temporary aggregation. Individuals were only included in these aggregations if they were within two body lengths (4 m) of other horses. Since data were collected on known individuals, age, reproductive state, genealogical relationship, dominance status and bodily condition were also noted and could be correlated with parasite levels. Dominance was determined from wins and losses during agonistic interactions, and based on pair-

Tab 1. Abundance of internal parasites. A (+) indicates that at least one member of the group emitted ova of that parasitic species, whereas a (0) indicates that no eggs were collected from the feces of any individual in a group. Groups are arranged by region, and approximate the linear arrangement of home ranges on the island. Mean total egg emissions differ significantly among harem on the eastern end of the island ($F_{9,24} = 3.11, p < 0.01$), but not on the western end ($F_{3,11} = 2.89, p < 0.09$). Ulysses' mid-east group is not shown because no larvae were cultured from his group. Nevertheless, the per capita egg production from this group is 2.6×10^4 . The percentage of animals sampled in a group containing all the parasites contained in that group represents a measure of similarity. Ba represents bachelor males. All other group are identified by the stallions's name.

Species	Location Group	West			Mid-East					East			
		Ap	Ju	Th	Sa	Po	Na	Da	Or	BH	EM	Ba	Ze
<i>Strongylus vulgaris</i>		+	+	+	+	+	+	+	+	+	+	+	+
<i>S. edentatus</i>		+	+	+	+	+	+	+	+	+	+	+	+
<i>S. equinus</i>		+	+	+	+	+	+	+	+	+	+	+	+
<i>Cylicocercus pateratus</i>		+	+	+	+	+	+	+	+	+	+	+	+
<i>C. goldi</i>		+	+	+	+	+	+	0	+	+	+	+	+
<i>Cylicodontophorus ultrajectinus</i>		+	+	+	+	+	+	+	+	+	+	+	+
<i>C. bicoronatus</i>		+	0	+	0	0	0	+	+	+	+	0	+
<i>Poteristomum</i>		+	+	+	+	+	+	+	+	+	+	+	+
<i>Triodontophorus</i>		+	+	+	+	+	+	+	+	+	+	+	+
<i>Gyalocephalus</i>		0	0	0	+	+	+	0	+	+	+	+	+
<i>Trichonema</i>		+	+	+	+	+	+	+	+	+	+	+	+
<i>Dictyocaulus arnfieldi</i>		+	+	+	+	+	+	+	+	+	+	+	+
<i>Parascaris equorum</i>		0	0	0	0	+	+	+	+	+	+	+	+
Total no. Species		11	10	12	11	12	12	11	13	13	13	12	13
Proportion of those sampled having all species		0.33	0.33	0.43	-	0.50	0	0.50	-	0	0.40	0	0
Mean number of ova emissions ($\times 10^3$)		0.6	2.7	2.7	2.3	4.4	4.9	3.0	3.0	4.0	2.0	3.3	6.0

wise comparisons, a strictly linear hierarchy emerged (Rubenstein, Hack and Waltman, unpubl.). Horses were either assigned a score based on absolute rank with 1 being the highest, or categorized based on relative rank. Those in the top, middle, and bottom third of the hierarchy were classified as having high, middle, and low rank respectively. Bodily condition was determined by the amount of fat on the rump (sensu Mulvany 1977, Pollack 1980). At one extreme, individuals in superb condition with well rounded shapes were assigned a score of 5, whereas at the other extreme, those so emaciated that the bones of the pelvis were easily seen, were assigned a score of 1 (see Rubenstein 1986 for details). All counts were log-transformed to improve normality.

Results

Internal parasites

Despite the difficulties that parasites face in maintaining themselves on oceanic islands, many intestinal species have managed to infect the horses of Shackleford Banks (Tab. 1). Of the 13 species identified, 4 of the 13 groups sampled contain them all, and none contain fewer than 10. Yet even within groups, which except for the bachelor groups consist of permanent members, different individuals are sometimes infected by different species. As Tab. 1 illustrates, at most 50% of the individuals sampled in a group contain the full compliment of para-

site species found in that group. And in about 25% of the groups, none of the individuals sampled is infected by all the parasites harbored by individuals living in that group. Moreover, variation among individuals in the total production of ova can also be quite large, ranging from a low of 50 egg to a high of 76,875 egg.

A variety of ecological factors affect the production of parasitic ova by the horses. Time of year is one. Total egg production is significantly higher in the summer than it is in the autumn ($x_{\text{summer}} = 3,678$ vs $x_{\text{autumn}} = 889$, $t_{77} = 3.9$, $p < 0.001$, Fig. 1), and even during the summer ova production declines slightly as the season

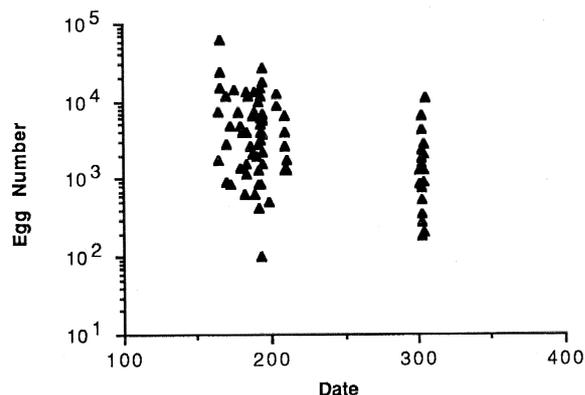


Fig. 1. Relationship between the number of ova emitted and days since the beginning of the 1984. The first cluster of points occurs in June and July while the second occurs in November.

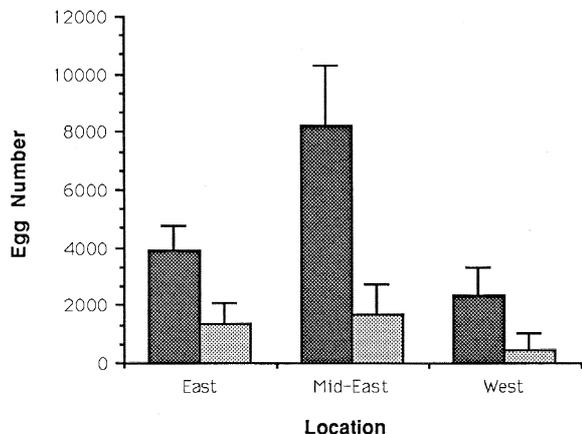


Fig. 2. Relationship between the number of ova emitted and location of a group's home range. Dark bars depict summer and light bars autumn. Both main effects are statistically significant (Location: $F_{2,66} = 4.85$, $p < 0.02$; Date: $F_{1,66} = 16.7$, $p < 0.001$), but not the interaction. Means and + 1 SE are shown in this and all other figures.

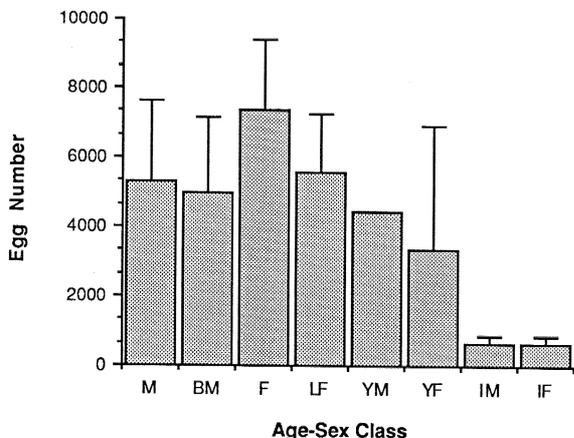


Fig. 3. Relationship between the number of ova emitted and age-sex classes. The classes are: Harem males (M), Bachelor males (BM), Non-lactating females (F), Lactating females (LF), Yearling males (YM), Yearling females (YF), Infant males (IM) and Infant females (IF).

progresses ($r = -0.27$, $p = 0.09$). Location on the island of a group's home range also has a significant effect ($F_{2,66} = 4.85$, $p < 0.02$). Horses living near the eastern end have higher total egg yields than those living at the western end (Fig. 2). This pattern holds even for the separate classes of parasites such as the strongyles, and *Dictyocaulus arnfieldi*, but it is especially pronounced for *Parascaris equorum* as none was found in any sample from the western end. Since no significant differences were found between the eastern and mid-eastern regions, these samples were pooled, and all subsequent analyses involve only samples collected during the summer, unless otherwise stated.

Of the three life history attributes, age, sex and reproductive state, only age significantly affects egg emissions ($F_{7,35} = 2.64$, $p < 0.03$, Fig. 3). Infants are significantly less parasitized than adults, but when they are removed from the analysis further age differences, such as between adolescents (2–3 yr olds) and adults, vanish ($F_{5,31} = 0.42$; $p < 0.83$). On average, males appear to be no different from females with respect to the total production of ova, and the differences between harem stallions and bachelor males as well as between lactating and non-lactating females seem to be small. The same pattern holds for strongyle, *Dictyocaulus*, and *Parascaris* egg emissions. Reproductive state differences occur among lactating and non-lactating females only with respect to the proportionate abundance of one larval species, *Cylicodontophorus ultrajectinus*. Lactating females exhibit 50% fewer larvae than non-lactating females (0.06 vs 0.13; $F_{5,31} = 2.67$; $p < 0.05$).

Mean total egg emissions differ significantly among harems on the eastern, but not on the western end, of the island (Tab. 1). To some extent these differences among groups can be explained by differences in opportunities for transmission. In both the western and mid-

eastern regions home range overlap can reach 77% which is much greater than the average overlap ($x = 23\%$) exhibited by the territorial harems further east. Nevertheless, others factors seem to be involved as well. The size of a group in which an animal resides, for example, accounts for approximately 16% of the variance in total egg production. Horses living in larger groups tend to produce more eggs than those living in smaller ones ($F_{1,27} = 5.12$, $p < 0.05$, Fig. 4). In addition, group size also seems to influence the relative mixture of parasites that individuals harbour. Whereas the proportionate abundances of *Cylicocercus pateratus* ($F_{1,27} = 7.01$, $p < 0.05$), *C. goldi* ($F_{1,27} = 15.6$, $p < 0.001$) and *Triodontophorus* spp. ($F_{1,27} = 3.71$, $p = 0.07$) increase as groups grow larger, those of *Strongylus vulgaris* ($F_{1,27} = 6.14$, $p < 0.05$), *S. equinus* ($F_{1,27} = 6.86$, $p < 0.05$) and *Trichonema* spp. ($F_{1,27} = 3.71$, $p = 0.07$) tend to decrease. In fact, for *Gyaloccephalus*, no larvae are

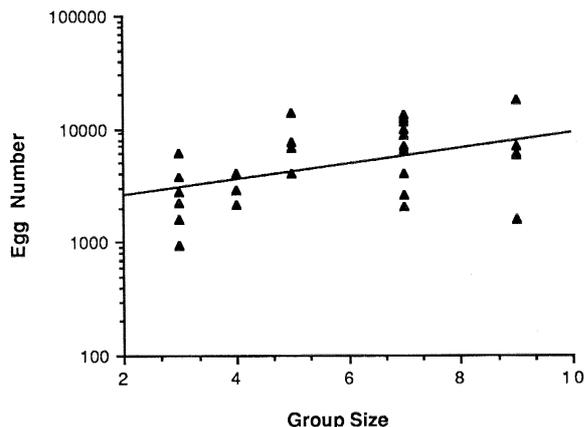


Fig. 4. Relationship between the number of ova emitted and group size.

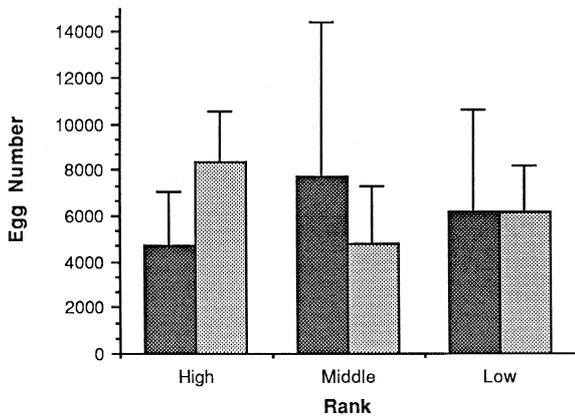


Fig. 5. Relationship between the number of ova emitted and dominance status. Dark bars depict males and light bars females.

found in the smallest harems at either end of the island, whereas in the largest harem it reaches an abundance of 0.20.

Dominance status appears to have little effect on ova emissions (Fig. 5). While dominant males seem to produce fewer eggs than middle or lower ranking individuals, the differences are small and, given the limited sample, not statistically significant. Moreover, the opposite trend appears among females, although again the differences are not statistically significant. No significant differences in proportionate larval abundances occur among individuals of differing rank, although dominant individuals of both sexes tend to have slightly, although not significantly, fewer larvae of *Strongylus vulgaris*, *Dictyocaulus*, and *Parascaris* than middle or lower ranking individuals.

The consequences of being infected with differing numbers of parasites appear to be quite dramatic. As Fig. 6 illustrates, bodily condition during the subsequent (1985) breeding season correlates negatively with the number of eggs produced during the end of this year's (1984) breeding season ($F_{1,24} = 4.71$, $p < 0.05$). Apparently horses with the lowest ova emissions during the summer tend to best be able to cope with harsh winter periods when foraging is difficult and as a result emerge in the spring with the best bodily condition.

Insects

On Shackleford, individual horses can be plagued by up to 200 flies at any one instant. Yet as Tab. 2 illustrates, the most important factor accounting for fly numbers is an individual's age-sex class. Adults are covered with significantly more flies than infants or even yearlings, but among adults, males tend to attract more flies than either lactating or non-lactating females (Fig. 7). Other factors such as time of day, habitat occupied, amount of sun shining, wind speed, group and aggregation sizes and, at least for females, dominance rank also play

significant roles in determining the number of flies an individual horse harbours. In general, horses tend to be covered by more flies on sunny days, when wind speeds are moderately high, when they occupy dune as opposed to swale or marsh habitat, and during the morning and early afternoon (Tab. 3).

Fly numbers are also negatively correlated with group size (Fig. 8). Horses residing in larger harems tend to be covered with significantly fewer flies than those living in smaller ones. In addition, the size of the temporary aggregations which form by harem members coming close together, also helps predict fly numbers (Tab. 2), but somewhat paradoxically the correlation is positive ($r = 0.31$, $n = 264$, $p < 0.05$). High levels of fly harassment appear to be associated with larger clusters of densely packed horses. Since horses tend to form tightly packed aggregations on sunny days and when winds are moderate to light, the positive relationship between fly number and the size of dense aggregations suggests that horses join together when flies are abundant, most active and particularly bothersome. Multiple regression analysis shows that this is indeed the case. When the effects of sky condition and wind speed are removed, the partial correlation between aggregation size and fly number becomes negative ($r_{\text{partial}} = -0.02$, $n = 109$, $p < 0.01$). Thus it appears that not only do individuals in larger harems experience reduced fly loads, but that when fly levels are high and flies are demonstrably causing a nuisance, individuals within harems can further reduce the burden by joining together into tight clusters. Since individuals in larger aggregations tend to make significantly more comfort movements than individuals in smaller ones ($r = 0.30$, $n = 264$, $p < 0.05$) it might appear that aggregating also assists in preventing flies from landing, biting and thus reducing fitness. But this is not the case. Horses generally make more comfort movements when fly burdens are heavy ($r = 0.61$, $n = 264$, $p < 0.01$, Tab. 2), and when the effects of sky

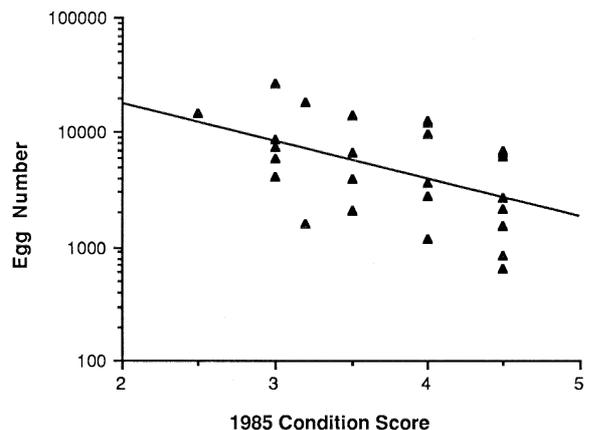


Fig. 6. Relationship between the number of ova emitted towards the end of the 1984 breeding season and bodily condition in 1985.

Tab. 2. Proportion of variation in fly numbers and numbers of comfort responses explained by environmental and social factors. None of the interaction terms is significant. Levels of significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Variable	Fly number		No. comfort movements		
	Proportion Variance explained	P Value	Proportion Variance explained	P Value	
Time	0.05	*	0.01	NS	
Wind	0.16	**		0.08	*
Sky	0.10	*	0.08	*	
Habitat	0.08	*	0.07	*	
Harem size	0.14	**	0.10	*	
Aggregation size	0.10	**	0.10	**	
Age-sex class	0.37	***	0.24	**	
Female rank		0.08		0.08	*

condition and wind speed are removed by multiple regression analysis, the effect of aggregation size on rate of preforming comfort movements vanishes.

At least for females, dominance status influences fly levels. High ranking females tend to be covered with significantly more flies than those of lower rank (Fig. 9). However, dominant females spend significantly more time within 2 m of stallions (Rubenstein and Hann, unpubl.). Since males tend to be covered by more flies than average females (Fig. 7), this rank effect may in part be the result of a differential ability to gain access to stallions, an ability that is itself mediated by rank.

Discussion

The horses of Shackleford Banks are infected by a variety of internal and external parasites. Not only do ova emissions appear to be considerably higher than those found in domestic horses or other feral populations (Pollack 1980), fly burdens also tend to be greater than those experienced by horses living in the Camargue (Hughes et al. 1981). Yet the burden, as revealed by the abundance of fecal eggs and larvae of intestinal worms

or counts of flies on or near horses, varies markedly among individuals. This variation is in part accounted for by a variety of environmental factors, particularly in the case of ectoparasites. Shackleford horses tend to be more harassed on sunny days, a result which mirrors the results of trapping studies by Schulze et al. (1975) and Hughes et al. (1981) showing that biting flies are more active when the sun is shining. Shackleford horses also appear to attract more flies when wind speeds are moderate, a pattern which is similar to that found in the Camargue horse population (Hughes et al. 1981). Presumably flies find it difficult, or energetically expensive, to travel in high winds, but it is not obvious why flies should fail to attack horses during still conditions. Perhaps light winds fail to transmit some of the cues that flies use for locating hosts.

Location influences a horse's burden of both ecto- and endoparasites. In the dunes fly numbers are generally higher than in the swale or along the fringes of a marsh. In part, these habitat differences are the result of differences in wind speed since dunes are effective baffles that can reduce even strong gusts to nothing but slight breezes. As a result, horses can reduce their fly

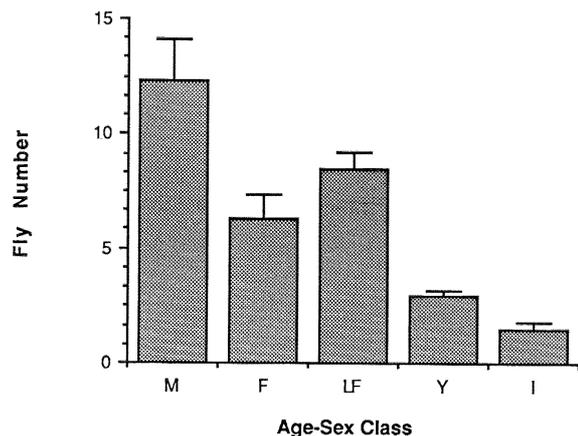


Fig. 7. Relationship between the number of flies and age-sex classes. The classes are: Males (M), Non-lactating females (F), Lactating females (LF), Yearlings (Y), Infants (I).

Tab. 3. The effects of sky conditions, wind speed (Beaufort Scale), and habitat on per capita fly number.

		\bar{X}	S.E.
Sky	Overcast	3.3	0.35
	Partly cloudy	19.3	1.80
	Sunny	22.4	1.60
Wind Speed	1	11.0	2.8
	2	6.0	0.6
	3	23.4	4.7
	4	15.1	1.9
	5	8.3	0.6
	6	12.0	1.5
		2.7	0.3
Habitat	Dunes	12.3	1.8
	Swale	8.5	0.6
	Marsh	8.9	0.6

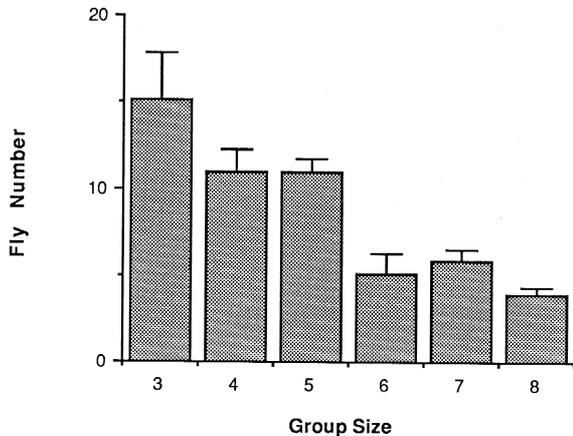


Fig. 8. Relationship between the number of flies and harem size.

loads by moving into more open habitats such as those found in the swale or march, particularly on sultry days. Such an ability to moderate fly levels by shifting habitats may, however, entail hidden costs. Since vegetation from all three zones must be consumed regularly (Rubenstein 1981), avoiding one zone to reduce fly harassment could result in a lowering of dietary quality. And horses, unlike grazing ruminants, do not have obligatory periods where they must cease foraging. Consequently, minimizing costs requires that any movement to fly free refuges must be coordinated with movements that either optimize foraging or coincide with periods where inactivity is favored. Presumably this is why Shackleford horses typically frequent the dunes late in the day when fly numbers are low, and sleep during extremely hot and sunny periods on the swale in open sandy areas, as do Camargue horses (Hughes et al. 1981), or near the edges of bodies of water, as do Assateague ponies (Keiper and Berger 1982).

The intensity of internal parasite infection is significantly lower on the western than the eastern end of the island. The effect is so dramatic that the ascarid *Parascaris equorum* is absent from the western population. In general the western end of the island is more saline and dung free. There the marsh habitat is restricted to the exposed tip of the island which is regularly submerged at spring high tides or whenever a strong north wind blows. As a result, the sea not only washes away feces, but also tends to cover the substrate with sand and salt, both conditions that reduce ova survival (Levine 1968). At least with respect to endoparasites, seasonality also has an effect on burden. Ova emissions are considerably higher during the summer than they are during the autumn.

Of all the factors affecting parasite burden, age is the most important. Infants are infected by significantly fewer worms, and are covered by many fewer flies, than either adolescents or adults. With respect to endopara-

sites, infants presumably have not been around enough to acquire large numbers of worms. With respect to flies, reduced levels could result from the fact that infants are smaller and have smaller surface areas than adults. Fly levels of adults are on average more than 8 times those of infants, however. Considering that most flies are located on backs and bellies, differences in surface area between adults and youngsters are not this large. Alternatively, since some insects locate their hosts by carbon dioxide emissions. (Wright and Kellogg 1962), infants may be relatively 'invisible' since they are less active and have lower metabolic rates than adults.

Differences in sex and reproductive state are more important in predicting fly loads than worm burdens. Again, differences in metabolic rate controlled by underlying hormonal differences may make males more easy to detect by biting flies than females, and lactating females more attractive than non-lactating ones. But the fact that metabolic and hormonal differences between harem and bachelor males, or between lactating and non-lactating females do not lead to differences in ova production is surprising. In other mammals, lactating females exhibit elevated fecal egg counts due to temporary depressions in immunological competence associated with altered hormonal levels (Connan 1972). Our results suggest that either the 'physiological costs' of lactation or of trying to break into the breeding hierarchy are not very large, or that horses on Shackleford are able to adjust their time and activity budgets in the short term to compensate for 'stress'. The idea that costs of breeding are insignificant is not likely to be true since females lose condition when they are lactating (Rubenstein 1986), and female mortality rates rise and surpass those of males once they reach sexual maturity (unpubl. data). The alternative, however, remains a possibility. On average, lactating females graze about 6% more per hour and take about 11% more bites per minute than non-lactating females, and stallions graze about 2% more than bachelor males.

That worm burdens do not vary significantly with

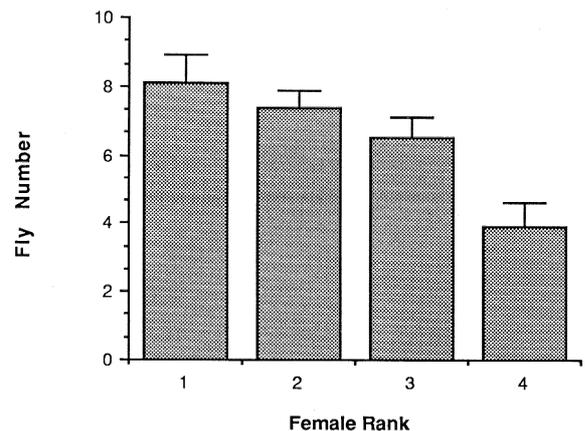


Fig. 9. Relationship between the number of flies and female dominance rank.

dominance status in this horse population is also somewhat surprising. Many other studies on mammals show that low status correlates with heightened susceptibility to infection and disruption of endocrine function (Christian and Davis 1964, Esch et al. 1975). Yet others such as Hausfater and Davis (1976) show that high ranking male baboons emit more ova than lower ranking ones, and that female ova emissions are only affected by reproductive state, not by rank. Apparently there is no universal dominance effect and as in the case of reproductively induced stress, some individuals may be able to minimize the effects of parasites by altering activity patterns. Clearly, more work is needed since the relationship between rank and reproductively induced stress is not straightforward.

The absence of a correlation between worm burden and male status has implications for the hypothesis that females choose males for their 'good genes' based on their overall health and vigor (Kodric-Brown and Brown 1984). Shackleford females search for and join dominant males, especially territorial ones, because only they can reduce harassment by other males and enable females to increase feeding and reproductive efficiency (Rubenstein 1986). Although dominant males do not display significantly lower worm burdens than subordinate males, territorial males, which as a class are the most dominant males on the island (Rubenstein 1986), do. Thus it is possible that females assess male quality and even the infectiousness of home ranges based on a male's behavioral vigor.

Unlike worm burden, fly levels do, however, correlate with female rank. But high ranking females may acquire their higher fly loads simply because they spend more time near stallions who typically carry more flies than average females. Proximity to males presumably has little effect on rates of worm infection since feces are deposited by all group members throughout the entire home range.

Of all the social factors, the number of horses an individual associates with is the most important in determining both endo- and ectoparasite burden. The effects of group size on each type of parasite, however, go in opposite directions. Although individuals in larger groups dilute their incidence of fly harassment by sharing the burden, they increase their worm loads by coming into contact with more infested dung. The effect of intestinal worms will be particularly severe if parasite genotypes change fairly frequently.

With respect to consequences of being infected, the effects of endo- and ectoparasites are quite different. Infection by intestinal worms seems to have a considerable effect on subsequent bodily condition, which in turn influences reproductive success (Rubenstein 1986), but has only limited influence on behavior. Observations show that horses have a tendency to defecate most often while travelling among grazing areas in patches of needle grass (*Juncus rosmarianus*), a species they do not eat. Conversely, ectoparasites appear to have no direct

consequences on bodily condition, but a substantial effect on many elements of behavior. When flies are abundant and active horses tend to increase the rate at which they perform comfort movements, move to relatively fly free refuges, and aggregate into tight clusters.

Yet despite this one important socializing effect, the influence of ectoparasites on structuring horse social organization appears to be minimal. Living in large groups reduces fly harassment, but the benefits can not be so great as to offset other costs of forming these associations, such as increased intestinal worm burden or even intensified competition (Rubenstein 1986). Otherwise, on days when flies are abundant and active individuals should be seen leaving small harems to join larger ones, or at least heavily plagued females should be seen leading their harems to associate with others. Neither of these behaviors is seen, even though 10% of all adult females change groups once a year (Rubenstein 1981), females initiate most group movement, and other species in the genus, in particular zebras, routinely form large, tightly clustered, herds composed of many harems (Rubenstein 1986). Moreover, the fact that dominant females tolerate high fly loads by associating with stallions suggests that the fitness costs associated with fly harassment may in fact be quite small, and that they are easily surpassed by other benefits of associating with particular individuals. Thus although both endo- and ectoparasites affect an individual's behavior, the fact that groups do not grow very large or merge into herds suggests that the debilitating effects of internal parasites is greater than those associated with external dipteran vectors. Even though fly burdens are reduced by forming larger and tighter groups, it appears that only endoparasites by increasing the costs of living in large groups actually influences the structure of horse society by limiting the growth of groups and by preventing the formation of herds.

Acknowledgements – We thank A. Keymer and A. Read for critical comments on a draft of the manuscript, the Duke University Marine Laboratory for their assistance while performing many phases of the project, and the fellows of Merton College for their hospitality and intellectual support. This research was financed by the National Science Foundation, grant number BSR-8352137, and the Dean of the College, Princeton University.

References

- Alexander, R. D. 1974. The evolution of social behavior. – *Ann. Rev. Ecol. Syst.* 5: 325–383.
- Berger, J. 1986. Wild horses of the Great Basin. – Chicago Univ. Press.
- Brown, C. R. 1985. Ectoparasitism as a cost of coloniality in Cliff Swallows (*Hirundo pyrrhonota*). – *Ecology* 67: 1206–1218.
- Christian, J. J. and Davis, D. E. 1964. Endocrines, behavior, and population. – *Science* 146: 1550–1560.
- Connan, R. M. 1972. The effect of host lactation on a secondary infection of *Nippostrongylus brasiliensis* in rats. – *Parasitology* 64: 229–233.

- Duncan, P. and Cowtan, P. 1980. An unusual choice of habitat helps Camarague horses to avoid blood-sucking flies. – *Biol. Behav.* 5: 55–60.
- and Vigne, N. 1979. The effect of group size in horses on the rate of attacks by blood-sucking flies. – *Anim. Behav.* 27: 623–625.
- Dunn, A. M. 1978. *Veterinary helminthology*. – Heinemann Medical Books, London.
- Esch, G. W., Gibbons, J. W. and Bourque, J. E. 1975. An analysis of the relationship between stress and parasitism. – *Am. Midl. Nat.* 93: 339–353.
- Espmark, Y. and Langvatn, R. 1979. Lying down as a means of reducing fly harassment in red deer (*Cervus elaphus*). – *Behav. Ecol. Sociobiol.* 5: 51–55.
- Freeland, W. J. 1977. Blood-sucking flies and primate polyspecific association. – *Nature, Lond.* 169: 801–802.
- Halvorsen, O. 1986. On the relationship between social status of host and risk of parasitic infection. – *Oikos* 47: 71–74.
- Hausfater, G. 1985. Baboons are ticked-off. – *Nat. Hist.* 85: 262–268.
- and Watson, D. F. 1976. Social and reproductive correlates of parasite ova emissions by baboons. – *Nature, Lond.* 262: 688–689.
- Holmes, J. C. 1982. Impact of infectious disease agents on population growth and geographical distribution of animals. – In: Anderson, R. M. and May, R. M. (eds), *Population biology of infectious diseases*. Springer, Berlin, pp. 449–455.
- Hoogland, J. L. 1979. Aggression, ectoparasitism, and other possible costs of prairie dog (*Sciuridae*, *Cynomys* spp.) coloniality. – *Behaviour* 69: 1–35.
- Hughes, R. D., Duncan, P. and Dawson, J. 1981. Interactions between Camargue horses and horse flies (*Tabanidae*). – *Bull. Ent. Res.* 71: 227–242.
- Keiper, R. and Berger, J. 1982. Refuge seeking pest avoidance by feral horses in desert and island environments. – *Appl. Anim. Ethol.* 9: 111–120.
- Kodric-Brown, A. and Brown, J. H. 1984. Truth in advertising: the kinds of traits favored by sexual selection. – *Am. Nat.* 124: 309–313.
- Levine, N. D. 1968. *Nematode parasites of domestic animals and of man*. – Burgess, Minneapolis, MN.
- , Mehra, K. N., Clark, D. T. and Aves, I. J. 1980. A comparison of nematode egg counting techniques for cattle and sheep feces. – *Am. J. Vet. Res.* 21: 511–525.
- Miller, W. C. 1953. The general problem of parasitic infestation in horses. – *Vet. Rec.* 65: 213–217.
- Mulvany, P. 1977. *Dairy cow condition scoring*. – National Institute for Research in Dairying, N. 4468.
- Pollack, J. 1980. Behavioural ecology and body condition changes in New Forest ponies. – Farm Livestock Advisory Committee, RSPCA.
- Rubenstein, D. I. 1981. Behavioral ecology of island feral horses. – *Equine Vet. J.* 13: 27–34.
- 1986. Ecology and sociality in horses and zebras. – In: Rubenstein, D. I. and Wrangham, R. W. (eds), *Ecological aspects of social evolution*. Princeton Univ. Press, Princeton, NJ, pp. 282–302.
- Schulze, T. L., Hansens, E. J. and Trout, J. R. 1975. Some environmental factors affecting the daily and seasonal movement of the saltmarsh greenland, *Tabanus nigrovittatus*. – *Environ. Ent.* 4: 965–971.
- Seyfarth, R. M. 1983. Grooming and social competition in primates. – In: Hinde, R. A. (ed.), *Primate social relationships*. Blackwell, Oxford, pp. 182–190.
- Talbot, L. M. and Talbot, M. H. 1963. The Wildebeest in Western Masailand, East Africa. – *Wildl. Monogr.* 12: 1–88.
- Tashiro, H. and Schwardt, H. H. 1953. Biological studies of horseflies in New York. – *J. Econ. Ent.* 46: 813–822.
- Wright, R. H. and Kellogg, F. E. 1962. Response of *Aedes aegypti* to moist convection currents. – *Nature, Lond.* 194: 402–403.