

Chapter 11

REPRODUCTIVE VALUE AND BEHAVIORAL STRATEGIES: COMING OF AGE IN MONKEYS AND HORSES

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I. ABSTRACT

Growing up in animal societies is not an easy task. Apart from the obvious hardships imposed by predators and the physical elements, each juvenile must contend with a complex social environment in which other juveniles and their parents attempt to increase their inclusive fitness at its expense. Since an individual's success or failure early in life will have dramatic consequences on its later reproductive success, this competition should be intense. The form it takes should be varied as youngsters of different ages, sizes, past experiences and physiological conditions should manifest different competitive abilities, and probably even different proximate "goals." Nevertheless, understanding why particular juveniles manifest particular patterns of development is far from obvious. The aim of this chapter is to examine how features of the social environment affect the activities of juveniles and their kin. It is easy to envisage juveniles adjusting their behavior so that it increases their chances of success in a particular environment. But kin should also adjust the behavior of their juvenile relatives for two reasons. First, juveniles represent the vehicles by which related adults can augment their own inclusive fitness. And second, juveniles are often less able than their adult relatives and thus are easily manipulated.

II. CONCEPT OF REPRODUCTIVE VALUE

Even if animals do not choose among strategic alternatives, natural selection does; behavior patterns that lead to the production of many offspring that survive to reproduce will be favored over those that do not. The allocation of resources to achieve greater reproductive success than a competitor is a complex problem. One dimension of the problem entails apportioning resources at one point in time among competing options. The other involves apportioning resources between present and future activities. For juveniles and their kin the second dimension is particularly relevant since commitment of resources at the right stage in development will have profound consequences on future reproductive success.

A convenient measure of an individual's future worth is Fisher's (1930) concept of reproductive value. In natural populations individuals of different ages contribute differentially to the ancestry of future generations. For most species fertility is highest and mortality lowest around middle age. For populations with discrete breeding periods assigning each age class its reproductive value can be accomplished by the equation,

$$V_x = \frac{\lambda^x}{l_x} \sum_{t=x}^{\infty} \lambda^x l_x b_x \quad (1)$$

where λ is the geometric growth rate of populations once a stable age distribution has been reached, l_x is the prospect of a newborn surviving to age x , and b_x is the fecundity of a female aged x . Essentially a female's reproductive value is the sum of her current reproduction plus her expected future reproduction discounted back to the present. For a population that has discrete generations and is not changing in size this equation can be further simplified to

$$V_x = b_x + \sum_{t=x+1}^{\infty} \frac{l_t}{l_x} b_t \quad (2)$$

which shows clearly the present and future reproductive components (Pianka & Parker 1975). The second term is the residual reproductive value which weights future fecundity by the probability of surviving to reproduce.

In general reproductive value of an individual will look something like Fig. 1. Reproductive value will be highest near the age of first reproduction because at this age an individual's expectation of future suc-

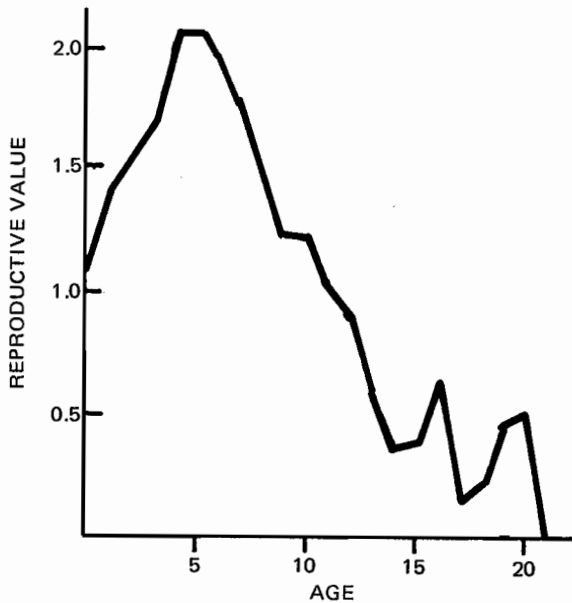


Fig. 1. Reproductive value at each age in rhesus monkeys living on Cayo Santiago (after Schulman and Chapais, 1980). The curve is representative of most long lived iteroparous mammals.

cess is at its greatest. Before the age of first reproduction, reproductive value is less than maximal because the prospects of surviving from birth to puberty are not 100%. After this age reproductive value declines with age because more and more of an individual's expected success becomes realized.

Until one decade ago the fitness consequences of age specific differences in reproductive value were largely ignored. Increasing inclusive fitness by performing or withholding altruistic acts depended on the worth of the potential recipient individual, but worth was only measured in terms of the coefficient of relationship (r), the likelihood that the individual possessed the same gene (Hamilton 1974). Emlen (1970), West-Eberhardt (1975), and Dawkins (1976) were the first to suggest that the benefits of assisting a young but distant relative might occasionally exceed the benefits of assisting a closer but decrepit relative. Thus, although degree of relatedness was still important, in populations with age structure and age specific reproductive expectations, it must be weighted by the probability

of the beneficiary actually producing offspring. In other words r must be weighted by the individual's reproductive value V_x . Furthermore, Milinski (1978) argues that the degree of altruism also depends on the reproductive value of the altruist since the cost of beneficence will be measured in lost opportunities to breed. Thus animals should be more altruistic when their reproductive value is low and less altruistic when their reproductive value is high. Conversely, animals should be selected to receive altruistic assistance when their reproductive value is high.

The recent work of Charlesworth and Charnov (1980) quantifies these relationships. They show quite clearly that when an act of altruism increases a recipient's chances of surviving from age x to $x + 1$ while decreasing those of the altruist, the reproductive values of the altruist (V_a) and beneficiary (V_b) in the following year ($x + 1$) modify Hamilton's condition for the spread of an altruistic gene so that

$$\frac{\text{benefit}}{\text{cost}} > \frac{1}{r} \cdot \frac{[V_a(x + 1)]}{[V_b(x + 1)]}$$

As seen in this relationship it is certainly true that these reproductive value considerations will have a profound affect on the behavior of altruists. But by using reproductive values simply as weighting factors, their importance is underestimated. When used in this fashion reproductive value serves as an attribute of each age class in the population, or at best, as an attribute of the "average" individual in each age class. Viewing reproductive value in this fashion obscures the fact that even within age classes individuals differ in their expected future reproductive success. Certainly a beneficent individual when confronted with a situation in which it can save only one of two identically aged and equally related kin, will save the one whose prospects of leaving the most viable offspring are higher. The choice might be based on any one of a variety of phenotypic attributes such as size, past experience, or dominance, but to a large extent the proximate criterion of choice is unimportant. What is important, however, is that the choice should ultimately depend on how much that altruistic act *augments* the reproductive value of each of the two possible recipients. Natural selection will favor directing altruistic acts to those individuals that will have the higher reproductive value *after* the altruistic act has been performed. For the same cost to the altruist, it is possible for an individual that had a lower reproductive value prior to the altruistic act, to end up with a higher reproductive value afterwards. Thus there should be times when individuals with lower initial reproductive values should be favored over those with higher initial reproductive values.

In general an individual's decision whether to support one individual over another will depend on the following criterion

$$\frac{\sum_{i=1}^n (V_i + \Delta V_i)r_i}{\sum_{i=1}^n r_i V_i} > 1 \quad (3)$$

where V_i is the reproductive value of the i th individual that ego interacts with, ΔV_i is the change in individual i 's reproductive value after ego has acted, and r_i is the coefficient of relatedness between ego and individual i . There are two important features of the criterion that should be noted. First, the criterion encompasses all n individuals in a community that ego interacts with, because even action directly affecting 2 individuals will often have ramifications affecting everyone in ego's social sphere. Second, the criterion requires that ego's inclusive reproductive value ($\sum_{i=1}^n r_i V_i$, *sensu* Shulman and Chapais, 1980) increase after the performance of the altruistic act. It is very likely that this will involve a decrease in ego's own personal reproductive value ($r = 1$), or those of other relatives. Clearly the strategy that makes the left hand side of the inequality as large as possible will be the one that augments ego's inclusive reproductive value most.

The way in which this criterion operates can be seen in Fig. 2. Here the reproductive value associated with seven age classes of feral female horses is depicted by the solid line, and the standard deviation about the reproductive value of each age class is depicted by the shaded area around the solid line. The horses live unhindered on Shackleford Banks, a barrier island off the east coast of North Carolina. Since 1973 I have been monitoring their social behavior, ecology, and demography. The survival and reproductive success of the first two cohorts of females born since 1973 have been followed for seven years. At each age every female's current and future reproductive success can be measured, and used to compute the average age specific reproductive value and its variance.

In a simple situation in which an individual (ego) can affect the reproductive value of only two equally related relatives, whether ego assists either relative will depend on whether ego's inclusive reproductive value is increased by its action. If its inclusive reproductive value can be increased by aiding either relative, then whom ego aids will depend on which one will have the highest reproductive value after the altruistic act is performed. If we imagine two individuals aged x and $x + 1$ and having

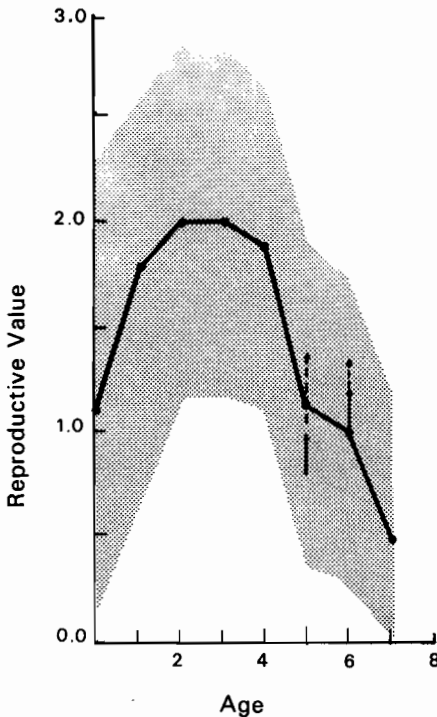


Fig. 2. Reproductive value curve for feral horses living on Shackleford Island. The solid line depicts average age-class reproductive value and the stipled area measures one standard deviation about the average. The curves are derived from females born in 1973 and 1974 during the first 7 years of life. The vertical solid lines denote the consequences of maternal actions leading to equal increases in reproductive value (ΔV), whereas the combinations of vertical solid and dashed lines represent maternal actions leading to unequal increases in reproductive value.

reproductive values V_i and V_j respectively, where $V_j > V_i$ (see Figure 2), then if ego's assistance would change the reproductive value of each individually equally then $V_j + \Delta V_j > V_i + \Delta V_i$ and ego should support the older individual. If ego's decision had been based on the average, or age class, reproductive value (\bar{V}_x) then he should have supported the younger individual, since $\bar{V}_x > \bar{V}_{x+1}$. Of course, if ego's assistance had been able to boost the reproductive value of i more than that of j , such that $\Delta V_i \gg \Delta V_j$ then $V_i + \Delta V_i$ might have surpassed $V_j + \Delta V_j$. Thus agreement with the average reproductive value prediction might have occurred, but for a different reason. As these two hypothetical examples illustrate, the direction of the inequality will depend on whether each additional unit of aid to an individual brings increasing, decreasing, or unitary returns, and whether this marginal rate of return is correlated with initial levels of reproductive value. In some cases, it will be individuals of low reproductive value that gain the most by a fixed level of assistance, whereas in other cases it will be those of high reproductive value.

Figure 2 suggests that juveniles may be the most likely to receive support. Since the range of possible successes or failures for young an-

imals exceeds that for older animals, the variance in reproductive value for juveniles will be greater than that of post-reproductives. As shown in the figure this is the case for female Shackelford horses. Therefore from ego's perspective the potential gain in inclusive reproductive value should be highest for assisting juveniles. In addition, the potential loss in ego's own reproductive value while augmenting that of relatives will decrease as it gets older. Thus ego may be able to increase its inclusive reproductive value more as it gets older, especially if it assists juveniles. Again, much will depend on the nature of the marginal gains, and how these are correlated with reproductive value and age.

Even without assistance, one's behavior may increase one's own reproductive value. Equation (2) suggests that there is likely to be a trade-off between current reproduction (b_x) and residual reproductive value (RRV). Although equivalent reproductive values can be obtained for a variety of combinations of b_x and RRV, it is likely that these parameters will vary in an inverse fashion. If investment in current reproduction leads to reduced survival, as it often does, then RRV should decline. Pianka and Parker (1975) depict this tradeoff graphically as in Fig. 3. When the curve intersects the abscissa, investment in current reproduction is total and RRV is zero. When the curve intersects the ordinate, no resources are invested in current reproduction. The optimal mixture of current reproduction and RRV which maximizes reproductive value at age x occurs at the point of tangency between the tradeoff curve and a line described by $RRV = V_x - b_x$. This equation is a rearrangement of equation (2), and describes a family of lines with slopes of -1 (present progeny are equal in value to future progeny in stationary populations). Since lines farther out from the origin have higher V_x , the point of tangency maximizes V_x . Thus an individual attempting to increase its reproductive value must alter the shape of the tradeoff curve so that the point of tangency shifts further out from the origin. Although this might occasionally be accomplished by behavior that leads to increases in both

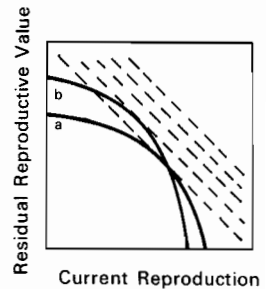


Fig. 3. Tradeoff between current reproduction and residual reproductive value. Curve (b) depicts a tradeoff yielding higher reproductive value than curve (a).

b_x and RRV, increasing reproductive value at any age will probably entail a reduction in one component of equation (2) and an increase in the others.

In theory at least, changes in behavior that change an individual's inclusive reproductive value should have important fitness consequences. But are there any examples of individuals in natural populations adjusting their behavior to increase their own reproductive value or that of a relative?

III. CASE STUDIES

A. Rhesus Monkeys

Detailed behavioral and demographic studies have been carried out on the free-ranging rhesus macaques of Cago Santiago Island continuously since 1956 (Rawlins, 1979). The population's diet is supplemented, but in other respects the animals live an unhindered existence. Typically females remain permanently in their natal groups whereas males disperse as they approach sexual maturity. Sade *et al.* (1977) has observed that whole families are arranged in linear dominance hierarchies. In other words, members of one family rank above all members of other families. The consequences of this dominance are dramatic. Using 10 years of life history data from La Parguera, Puerto Rico, Drickamer (1974) showed dominant females produced more offspring in a lifetime than did subordinate females. Sade also showed for the Cago Santiago colony that high-ranking families have a higher intrinsic rate of increase than lower-ranking families. There is also a social hierarchy within each family with the mother exercising dominance over her daughters. Thus a female ranks above all females to which her mother is dominant and ranks below all females to which her mother is subordinate. Interestingly, within a family rank varies inversely with age among sexually mature daughters. As a daughter reaches sexual maturity (age 4) she rises in rank above her next oldest sister. She maintains this rank until her younger sister reaches sexual maturity and surpasses her. Thus, dominance in rhesus monkeys is neither a fixed, nor an inherent attribute of an individual. Support from others can boost another's rank and increase the assisted individual's success in present or future conflicts. Such is the case in macaques as well as in langurs (Hrdy and Hrdy 1976), savannah baboons (Moore 1978) and gelada baboons (Dunbar and Dunbar, 1977). Recently Schulman and Chapais (1980) have noticed that rhesus macaques mothers withdraw their support from an older daughter and give it to a younger daughter as she

approaches sexual maturity. The timing of this transfer of support seems to suggest that mothers are maximizing their reproductive value by supporting the daughter with the highest reproductive value (see Figure 1). By constructing a simple model, Chapais and Schulman (1980) were able to show that such a strategy would increase a mother's fitness over the alternative strategy of continuing to support an older daughter with a lower reproductive value. They also constructed other models that showed that it was in every female's interest to support the youngest sexually mature daughter of every female relative. This remarkable result provides a theoretical framework for the incredibly stable hierarchically structured matriarchal society that rhesus macaques display.

At first glance this result seems to suggest that females react only to a daughter as an average member of an age class with a fixed reproductive value. Careful inspection of Chapais and Schulman's model, however, shows that the criterion for maternal support is based on the fact that when dominant, a daughter obtains her full age-specific reproductive value, whereas when subordinate, a daughter only receives a fraction of her age-specific reproductive value. This relationship is generated by the use of weighting factors that are valued at one and less than one for a dominant and a subordinate respectively. Thus in effect, the model implicitly assumes that a mother's support will affect each daughter by an identical amount. Although Schulman and Chapais scaled their reproductive value by diminishing it multiplicatively, the same results would have been obtained had they added ΔV to the younger daughter as she achieved dominance and subtracted ΔV from the elder daughter as she fell in rank. The important point to note is that the assistance of mother macaques seems to affect all daughters equally. Regardless of a beneficiary's age or any other attribute of her phenotypes, a mother's assistance always boosts reproductive value by the same amount. Whether maternal aid can affect daughters (or any other kin) differently depending on their phenotype, as formulated in equation (3), should be examined in other free living animal populations.

B. Feral Horses

So far we have examined a case where maternal support occurs because a mother's inclusive reproductive value is increased in ways which are in accord with the criterion expressed in equation (3). Are there any instances where individuals, especially juveniles, condition their behavior on the social environment, adjusting it in ways that alter their chances of survival, or reproductive prospects, and increase their repro-

ductive value? On Shackleford Banks, juvenile horses of both sexes, appear to adopt alternative patterns of development which boost their reproductive value.

Horses typically live in groups. Some live in harems which are composed of adult females, their young, and a single stallion. Other live in bachelor groups which are much less stable, and are only composed of males. When juveniles of both sexes begin to breed, which on Shackleford occurs at about three years of age for females, and at about four years of age for males, they leave their natal groups. When they do so, they are confronted with a variety of options. At the age of sexual maturity, young males have been seen to (1) join bachelor groups, (2) join other harem groups as subordinate males, taking over some of the tasks of the herd stallion, and (3) remain in the natal group as subordinate helpers. For females, there are fewer options, as all females quickly attempt to integrate themselves into new harems. Nonetheless, they have options since they wander widely before selecting a particular group to join. I will show that the one common feature about all these behavioral variants is that depending on the demography of both a particular group and the population as a whole, the behavior adopted by each juvenile always appears to be the one that (a) results in a higher reproductive value than any other option in those conditions and (b) if chosen under different conditions would result in a lower reproductive value.

On Shackleford Island juvenile males leave their natal areas at about four years of age. They are not driven out by either adult males or females; rather they leave of their own accord. Usually they leave alone as no other male sibling from their cohort, or from the one preceding or following theirs, has survived. This is because on Shackleford the likelihood of any individual surviving to two years of age (the highest observed age at weaning) is 48% (Rubenstein, 1981), and for males it is only 41%. From cohorts born in 1973, 1974, and 1975, only eight of 22 males survived to four years of age, and six of these left their natal group alone. Only one group had two males within one years of age of each other survive to the age of independence. When this age arrived they left their natal group as a pair, even though one of the males was only three years of age. What is most interesting about these eight males is that their developmental histories differ and appear to covary with differences in reproductive value.

All six males leaving their native groups singly first went to the territorial boundary separating their natal area from that of a neighboring harem. There they grazed for less than a week. Approaches, and even attacks, by the neighboring resident stallions were not uncommon, but usually the interactions were not severe. The juveniles, which were both

smaller and subordinate to the stallions, galloped away, often retreating into their natal territories. Eventually, however, these contests became more frequent and four of the six solitary juveniles moved to other more distant territorial borders. Since the same sequence of events occurred there, the juvenile males were forced to move again. Finally, they arrived in the area where the bachelor males (≈ 10) resided. Bachelor groups are small, usually consisting of two or three males, and movement of individuals among groups occurs daily. As a consequence these groups show little coordination during most activities, especially during conflicts involving approaching wanderers. In addition, low-level dominance scuffles commonly occur among bachelor males.

When each of these four juveniles arrived in this area, they did so alone. Although they were chased and attacked by resident bachelor males they could retreat and hide in the dense forest which surrounds the area in which the bachelor males congregate. Within a week, however, the intense chases, and kicking fights had disappeared and were replaced by more subtle dominance squabbles using sounds, ear movements, and rump pushes. Once the situation had settled down after each juvenile arrival, it was clear that the juvenile had been integrated into bachelor male society as he grazed, groomed, and moved with the others. But in every case the juvenile occupied the lowest rank in the hierarchy. How low depended on the year, as the size of the bachelor population varied among years. Never did a juvenile obtain a rank higher than 9. The consequences of low rank are many. Access to water is limited as dominants always arrive at a water hole first. Not only do they drink first but they also drink longest. Since the bachelor area is shared by two non-territorial harems (Rubenstein 1981) late comers which are subordinate are often driven off by harem stallions before they can get a full supply of fresh water. Furthermore, low ranking males are often harrassed and supplanted from good feeding areas by dominants, and their body condition is usually poorer than that of a high ranking male. In general, the death rate of males decreases dramatically after three years of age. Nonetheless, one of the new bachelor males from this three year sample died within six months after arriving in the bachelor area. It is interesting to note that this male lost its mother when it was 14 months old and had left its natal area somewhat prematurely at age of 26 months. It was obviously smaller than all the other males, lost condition, and died during the first winter after its arrival in the bachelor areas.

The other two males leaving their natal groups singly behaved differently from the males described above. Both went to the edge of their natal territories as did the others, but went no further. One managed to stay on the periphery of the neighboring stallions' territory and slowly

moved closer to the group of females. The stallion repeatedly attempted to drive him off, but the juvenile was large for its age and very agile. Eventually it integrated itself into the group and fed near the females. Once in the group, the stallion's antagonisms decreased. Occasionally the juvenile male would aggressively engage neighboring stallions while protecting the harem much like the stallion. Usually, however, he would urinate on female urine and defecate on female dung immediately after they had scent-marked. In effect the juvenile male had become a subordinate helper male in his new harem. His activities freed up time for the stallion to graze and defend the territory from intruder males. Both of the subordinate male's activities cut into his foraging time. These costs seemed to be minor, however, and at least in theory, may have been offset by the fact that the male may have increased its chances of taking over the harem, as apparently occurs in waterbuck (Wirtz 1980). Furthermore, on one occasion the helping male managed to copulate with a female while the stallion was away. Although the stallion also copulated with the female after it returned from its territorial encounter, subordinates may in general achieve some reproductive success by serving as "helpers."

As for the other male who stayed on the edge of its natal group, he returned to his natal group after 11 days. He too covered the scent marks of the females and occasionally helped defend the territory from intruding males. He was never seen to copulate with any of the estrous females, however.

It is important to note that for both males the role of secondary helper was only temporary. Within eight months, both these secondary, or helper, males were driven from the harem groups by the stallions. They went directly to the bachelor area, although at different times, where they joined the bachelor males. Possibly because the breeding season was over when they arrived and aggressive levels were low, possibly because their bodily condition improved on the better vegetation of the territorial harem areas (Rubenstein, 1981), or possibly because their fighting experience in the harems improved their fighting ability, they entered the hierarchy not at the bottom but somewhere in the middle.

Of the six males leaving their natal group alone, those going directly to the bachelor area did least well since they obtained the lowest ranks. In such ranks they were most likely to perish, and least likely to sneak copulations with females inhabiting the two neighboring nonterritorial harems. Furthermore, it will take them longest to reach the highest ranks. During the study, only two α and one β ranking bachelor males ever took over a harem. Thus it appears that the reproductive values of the four

males arriving directly from natal groups will be lower than those of males having temporarily resided in harems.

There are demographic reasons, however, why it is likely that these males could not have done any better. On Shackleford it appears that in two-thirds of the harems the change over of stallions occurred during one year. By the time the juvenile males from the 1973–75 cohorts left their natal areas these take-over stallions were in prime condition. The number of adult females in their groups were increasing, and the number of agonistic encounters with neighboring stallions had dropped (Rubenstein, 1981). They were strong and their positions were stable. Young wandering males, being no match for these stallions, probably behaved in a way that yielded the highest reproductive value possible.

For the other two juveniles that ultimately joined the bachelor groups alone, the demographic situation in the vicinity of their neighboring territories was very different. In one case, the neighboring stallion was old and losing females to the other younger more vigorous neighboring stallion. In the other case, the natal stallion had just taken over the group and was young and inexperienced. He too was losing adult females to a neighboring stallion. In both cases, the juvenile males wandered into a situation in which they could apparently profit by staying and not going to the bachelor areas directly. Although they incurred some costs while residing in these territories for a few more months, the benefits they derived were apparently large, as they took places among the bachelor males at ranks higher than those of the “average” newcomers.

Of the eight males, two left the group as a pair. These males ultimately arrived in the bachelor area together. There they moved, groomed, and grazed together. When approached by the loosely organized bachelor groups the pair showed greater cohesion and often drove off the bachelor males. They also successfully supplanted established bachelors from water holes, and good grazing sites. Possibly as a result of their abilities, when they joined the bachelor male society they acquired ranks in the middle of the hierarchy. What is interesting, however, is that the three-year-old male who left his natal group relatively early obtained such a high rank, especially since the other under four year old mentioned earlier left his harem alone, obtained a low rank, and perished during the following winter.

One of the striking aspects of the coincidental fact that two males close in age survived to the age of independence in the same harem, is that their behavioral development was very different from those of other juveniles maturing singly. Based on instantaneous-scan sampling, yearling males are significantly more active than yearling females. On average

they spend 20% more time per hour engaged in running than females of equivalent age. Although there have only been two instances of two males growing up together in eight years, activity data for both pairs when they were yearlings shows that on average each male spends about 50% more time per hour running than males maturing singly. In addition, pairs of males play fight frequently, and often these encounters escalate into serious fights in which vocalizations are heard. Sometimes minor injuries are sustained, as short periods of limping after such bouts of play have been recorded. Thus as Fagen (1981) has suggested two young males growing up together may have developed skills and motor abilities that they otherwise would not have developed growing up alone. Perhaps because these similar age pairs are preferential grooming partners, they often elicit activity from each other. But regardless of what factors actually increase the likelihood of play, the coordination and skills developed apparently result in long term benefits as these males enter the bachelor hierarchy with higher ranks than most of the other males of equivalent age reared alone. Although lifetime reproductive success for these particular paired males cannot be measured as they have not yet established harems, they are now nearing the top of the hierarchy. Interestingly, they are doing so sooner than some older counterparts raised alone. Since top ranking males often engage in sneak matings with neighboring females, and are the ones that take over harems, it should not be long before the reproductive success of males raised together increases rapidly. Thus because of a demographic "accident" these males have probably augmented their reproductive value far in excess of the other young males born into their cohorts. Furthermore, since the paired individuals were half brothers, each individual of the dyad will supplement its inclusive reproductive value by 25% of the others' enhanced reproductive value.

IV. DISCUSSION

The purpose of this chapter was to examine what factors influence the behavioral development of juveniles. Since not all youngsters in a population will have the same likelihood of surviving to old age, or the same success at reproducing along the way, youngsters will show differing reproductive values. If youngsters by themselves, or with the aid of close relatives, especially parents, can augment reproductive value it may pay them to do so as long as the sum of their own reproductive value and those of relatives when devalued by the appropriate coefficient of rela-

tionship increase as specified by equation (3). As Fig. 2 reveals, the greatest variance in reproductive value, and hence the greatest gains associated with changing an individual's reproductive value, occur at the youngest ages. Thus it should be juveniles that are most likely to receive aid, or adopt alternative paths of behavioral development. Conversely, older animals manifest smaller variances in reproductive value and therefore have the least to lose by being altruistic to younger relatives.

Increasing an individual's reproductive value may occur solely by increasing survival prospects. The reason that reproductive value of juveniles increases and peaks near the age of reproduction is that juveniles are most vulnerable during this period. Thus one might expect that juveniles, or their kin, will adopt behavior that reduces risks. Possibly this is why female prairie dogs (Hoogland, 1982) and ground squirrels (Schwagmeyer 1980) increase alarm calling just after weaning a litter. Hoogland's experiments involved pulling a stuffed badger by the burrows of females before and after a litter was weaned. In both experimental groups some of the mother's sisters were present as well. Sisters and daughters are equally related to the mother, but it seems reasonable to assume that at least some of the older sisters would have had higher reproductive values than the recently weaned young. That the mother alarm called more readily in the presence of the younger, presumably less "valuable" but more vulnerable individuals suggests that she may have been giving the alarm calls because they could have augmented the reproductive values ($+\Delta V$) of her daughters more than those of her sisters.

A juvenile's reproductive value can also be augmented by increasing current or future reproductive success [$(b_r$ of equation (3)]. This appears to be the case in rhesus macaques, where mothers support their daughters at about the time they begin to reproduce, and they maintain this support for approximately four years until a younger daughter becomes sexually active. According to Schulman and Chapais this gives the young female a reproductive advantage. Horses also seem to adopt developmental tactics that augment their fecundity. First, males remain in their natal territories for about one year longer than do females. During this time they derive significant foraging benefits that would not be possible in the nonterritorial area of the island where harem and bachelor males share grazing swards (Rubenstein, 1981). Possibly as a result their growth rate and bodily condition are high. These phenotypic characteristics should increase both future fecundity and survival. Second, for males that have other male companions, play fighting appears to increase their combative skills so that they enter the bachelor hierarchy with fairly high ranks. Thus it is likely that they will acquire sneak matings or harems sooner than peers not engaging as frequently in play fighting.

In none of the field studies examined in this chapter did an ontogenetic change in behavior entail an abandonment of, or delay in, reproduction. Such a strategy is possible, and might augment reproductive value substantially. This would be the case if the costs of reproducing when too young are high, and a delay might significantly enhance a juvenile's prospects of survival. Furthermore, during the delay a juvenile may even help a close relative rear its offspring. If the costs of helping are minor then the act of assisting a relative might not only increase a juvenile's inclusive reproductive value by increasing the reproductive value of the relative, but also by increasing its own residual reproductive value through skills acquired during this period. The importance of this tradeoff is examined at greater length by Macdonald and Moelhman in Chapter 10 of this volume.

When animals attempt to increase their own inclusive reproductive value they may have to withdraw support from others, or behave in ways that lower the reproductive value of others. From ego's perspective this may be necessary, but when this happens a conflict of interest will develop between these two individuals. If the interaction is between parents and offspring the parents' interests are more likely to prevail since they are often larger and more experienced and can manipulate their young (Alexander, 1974). This appears to be what occurs in the Shackleford horses as mothers manipulate daughters to increase their own inclusive reproductive value. The conflict arises because grazing competition on Shackleford is very intense. Despite the fact that horses spend over 75% of each hour grazing, bodily condition remains poor, and juvenile death rates remain high (Rubenstein, 1981). To ameliorate these consequences, territorial horses rotate grazing patches within certain vegetation zones which increases their grazing efficiency (Rubenstein, 1981). But as groups get larger and animals get bigger, the demand for forage increases and disrupts this grazing rotation. To reduce the intensity of grazing competition, group size must be reduced. Apparently to do this adult females drive two- and three-year-old females away from the feeding areas and eventually away from the group. It is interesting to note that based on changes in reproductive value young females should be those individuals least affected by this behavior. After they are driven from the natal territory they will join another harem, most likely on a territory, and derive substantial feeding benefits. At least from the mother's viewpoint the gains her daughters can expect, *on average*, to obtain elsewhere are not likely to be lower than those they would have obtained had they remained in the natal territory. In addition since the size of the group has been reduced the mother's gain will have increased. By excluding juvenile females fairly early in their development a mother can apparently augment her inclusive reproductive value. Such a tactic would only be

successful if the mother could exclude the ostracized daughters of females from other harems. It is interesting to note that as strange juvenile females enter a territory adult females attempt to drive them away. Often the territorial females are successful at repelling young wandering females, but persistent support by males in their prime (9–11 years old) can overcome the concerted efforts of the females.

Mothers, and even fathers, rarely drive off males, however. By doing so parents would probably lower their own inclusive reproductive value. Since only males that are in good condition will rise rapidly to the top of the bachelor hierarchy, these males should be the ones that obtain harems and achieve disproportionate reproductive success at an early age. Banishing males at too young an age to the bachelor area where resources are poor, most likely would lower their future reproductive value. On the other hand, letting them remain on the good grazing grounds an extra year may significantly augment their reproductive value. Allowing them to remain any longer, however, would mean that these young males would be reproductively active on their natal territory. This might put them in reproductive competition with the dominant male (usually their father), and lead to the possibility of close inbreeding. Either event might lower a parent's inclusive reproductive value and should lead to the eventual expulsion of the young males by the parents. In fact, by five years of age all males are driven from their natal areas. From these two examples it appears that manipulating an individual's reproductive value may lead to conflicts of interest among parents and offspring, but not in all cases. Whereas a conflict develops between a four-year-old female and her mother, none apparently develops among a four-year-old male and either parent.

These observations on the ontogeny of feral horses on Shackleford Island suggest that aspects of the social environment, particularly the number of similar aged peers, and the number, age, and ability, of the harem stallions in the population, affect both the course of an individual's development and its reproductive value. It is possible that the behavior of the horses on this island is somewhat atypical, especially since the population is not large, and the high juvenile mortality rates reduce the infant and juvenile age classes further. Nevertheless these observations suggest that horse behavior may follow simple rules during development that are conditioned on the environment, and change in ways that tend to increase inclusive reproductive value. For males the simple rule is "to disperse at about four years of age and attempt to enter a neighboring harem." If the demography of the overall population is such that there are some old deteriorating males nearby, then the dispersing youngsters might succeed at this strategy—at least for a short while. If they can not integrate themselves into a harem, then they do the only thing possible.

which is to associate with the bachelor males. Usually this means initially adopting a low rank and suffering the consequences attached to this status. Even males that temporarily succeed in integrating themselves into harems ultimately end up with the bachelor males. They seem, however, to profit by their experience and obtain higher initial ranks. Such benefits may also accrue to those youngsters fortunate enough to have a peer of the same sex and the same age present in their natal group while growing up. For them the same rule appears to apply, but for reasons that appear to be associated with altered patterns of socialization, each individual in the departing pair obtained a higher initial rank in bachelor society than males entering bachelor society alone and directly from a natal group.

V. SUMMARY

The behavioral development of individuals can be affected by many facets of the social environment. Since not all youngsters in a population will have the same likelihood of surviving to old age, or the same success at reproducing along the way, youngsters of the same age will manifest different reproductive values. If youngsters by themselves, or with the aid of close relatives, especially parents, can augment reproductive value it may pay them to do so as long as the sum of their reproductive value and those of relatives devalued by the appropriate coefficient of relatedness is increased. In theory the greatest variance in reproductive value, and hence the greatest gains associated with changing an individual's reproductive value, should occur at the youngest ages. Thus it should be juveniles that are most likely to receive aid, or adopt alternative paths of behavioral development. Conversely, older animals should manifest smaller variances in reproductive value and therefore should have less to lose by being altruistic to younger relatives. That rhesus monkey mother withdraw support from an older daughter to assist and augment the reproductive success of a younger daughter as she reaches puberty appears to support this conclusion. Additional support comes from the fact that juvenile feral horses disperse differently depending on their socialization history and on the age distribution of harem tending males, and that these patterns affect reproductive value.

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