

Life history and social organization in arid adapted ungulates

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Introduction

Animals that live in deserts appear to be special. They have to cope with extremely high temperatures during the day and extremely low ones during the night. And given limited and unpredictable rainfall, the resources they depend on are likely to be highly variable in their temporal abundance and spatial dispersion. But is the behavioral ecology of arid adapted animals special? In particular, are there special ecological features of extremely arid environments? And if so, do they lead to novel foraging, fighting, mating and reproductive behavior? By examining species that vary in size, mode of temperature regulation and trophic level, the articles in this section address these questions and provide a basis for developing generalizations concerning the 'uniqueness' of the behavioral ecology of desert animals.

Behavioral ecology is the study of the adaptive value of behavior. As is the case for any adaptation, behavior that enhances an individual's survival and reproductive prospects is shaped by natural selection in relation to environmental conditions. Thus to understand how behavior helps an individual to survive by avoiding predators and exploiting critical resources, or to enhance its reproductive success we must understand the individual's ecology. In particular, we must know what foods an animal eats, what enemies it must avoid, what are its breeding requirements and what other members of its population are doing. It is the central theme of behavioral ecology that in particular environments some behavioral and life history patterns will be better than others, and that what determines which are best is the distribution of these critical ecological elements in both space and time.

Perhaps the best examples of behavior being an adaptation to a particular environment are those connected with reproduction. The evolution of both investment strategies and life histories of females, and mating strategies of males have been shown to be linked to ecological pressures in many species. This article examines whether the particular reproductive and subsequent social patterns of ungulates living in arid habitats differ significantly from those living in mesic ones. I will begin by outlining the basic tenets of life history and mating system theory. Then using environmental features of arid habitats I will use the theories to make predictions about what life history and mating patterns should occur under extremely arid conditions. Finally, comparisons of closely related species, and even different populations of one species, living in habitats of varying aridity will be used to evaluate the accuracy of the predictions.

Theories of life history and mating system evolution

For many animals, and in particular for most mammals, only the reproductive success of males, not that of females is limited by number of matings. Since sperm is rarely limiting, number of copulations has little effect on the ability of females to augment their reproductive output (Bateman, 1948; Trivers, 1972). Rather, the reproductive success of

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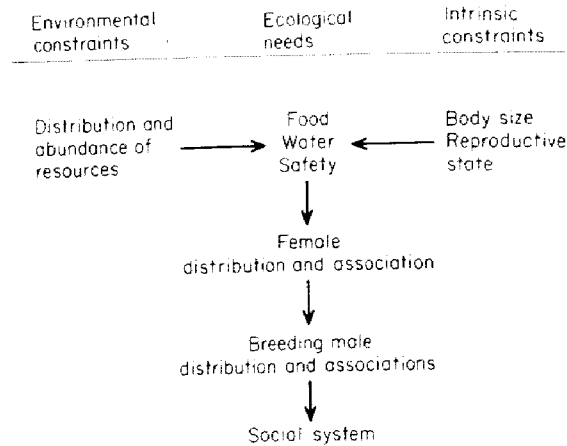


Figure 1. Model demonstrating how social organizations develop. Internal constraints determine how important are particular ecological needs, and environmental patterns influence female spacing which in turn influences male behavior. The interaction among male and female behavior determines the social system.

females is determined by the ability to acquire food, water, and find safe sites for rearing offspring. Thus the differences in the reproductive behavior of the sexes are profound. Whereas males are limited by availability of females, females are limited by availability of critical ecological resources. Two important consequences arise from this relationship (Fig. 1). First, the abundance and distribution of these critical resources will shape female movements, associations and competitive relationships as well as the extent to which resources are invested in reproduction as opposed to maintenance. Second, the distribution and association of females will determine the reproductive tactics of males, and thus the mating system. Therefore, if the distribution of critical resources in deserts is special, then unique life history patterns (female response), and mating systems (joint response) should occur. Alternatively, if animals living in arid environments are already pre-adapted for this existence, these 'special' or 'harsh' conditions may only be myths of our making, not the reality that the animals themselves perceive. As a result, no unique life history or social responses should occur.

Life histories

The fundamental tenet of life history theory is that the ratio of inescapable adult to juvenile mortality tends to bias populations to one of two extreme selective regimes (Horn & Rubenstein, 1984). High, or variable, adult mortality favors early breeding, high fecundity, rapid development and small adult size, even if this leads to increased sensitivity to environmental vagaries. Low, or constant, adult mortality, however, often leads to crowded populations where reproduction is difficult and a premium is placed on competitive ability. In such populations selection favors parents that conserve resources and invest them in themselves or a few well-endowed offspring. It is important to note that high levels of inescapable juvenile mortality cannot be reduced by additional parental investment. Investments that parents make are investments that will enhance a surviving offspring's chances of succeeding as adults as they attempt to enter the breeding population.

Mating systems

The fundamental tenet of mating system theory is that the distribution of females constrains male mating options. Emlen & Oring (1977) proposed that polygyny would

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occur whenever males could be emancipated from providing parental care, and that the form of polygyny that would evolve depended on ecological factors. When females were in groups they argued that males would defend groups, but when the resources females required were in patches males would defend patches, mating with receptive females as they arrived. If neither females nor the resources they needed were clumped, then as a last resort males would search for individual females and use dominance to obtain access. While this model provides a useful framework, it fails to show explicitly how different ecological conditions influence female movements and associations. Consequently, it does not provide a quantitative means of predicting male behavior. But it can be easily expanded to do so.

If female movements have been optimized to acquire food and water and natural selection favors males that maximize encounters with receptive females, then males have two main options. They can either follow females that are alone or in groups, searching for those that are receptive, or they can defend a territory containing the resources that females require, and wait for females to visit before mating with the receptive ones. To determine under what conditions selection would favor one strategy over the other, consider a habitat that is a mosaic of vegetation patches in which some of the vegetation is dense, whereas in others it is sparse. Now imagine that a sedentary or territorial male has a territory containing a proportion p of dense vegetation and a proportion $1 - p$ of sparse vegetation, whereas a mobile or following male has a home range with only a proportion p' of dense vegetation and a proportion $1 - p'$ of sparse vegetation. Also imagine that on dense vegetation females move slowly and linger for a long time, whereas they travel quickly when foraging on vegetation that is sparse. If the likelihood of a male mating with a female is proportional to how much time he associates with her, then the reproductive gain associated with having access to dense vegetation will be G and will be greater than that associated with sparse vegetation which will be B . If the cost associated with a territorial male's ability to keep all other males away from a female is C , then the gain to a territorial male is

$$P_1 = pG + (1 - p)B - C$$

and the gain to a mobile male is

$$P_2 = p'G + (1 - p')B.$$

For territoriality to be favored over wandering $P_1 > P_2$ which occurs when

$$(p - p')(G - B) > C.$$

In general, when territorial males are disproportionately able to control densely vegetated areas $p - p' \gg 0$, and the net reproductive benefit of having access to good grazing swards is large $G - B \gg 0$, territoriality is favored.

Since most species of antelope inhabiting mesic environments exhibit territoriality (Jarman, 1974) it is instructive to determine under what conditions territoriality should break down. The first occurs as the costs of maintaining exclusive control of an area increase. If costs are proportional to the number of intruders in the population and only a limited number of viable territories are possible, then as the sex ratio (males/females) increases the likelihood of territoriality should decrease. The second condition occurs when sparse patches of vegetation are large and very common. If the likelihood of a copulation and paternity certainty are associated with how long a male associates with a female, then the steady state proportion of females in densely vegetated areas is

$$x = x(1 - a) + (1 - x)b$$

$$x = \frac{b}{a + b},$$

and the proportion in the sparsely vegetated areas is

$$y = I - x,$$

where a is the likelihood of a female in a dense habitat moving into a sparse one, and b is the likelihood of a female in a sparse habitat moving into a dense one. If $G \propto x$ and $B \propto y$, then only when $b > a$ will $G - B > 0$, a necessary condition for territoriality. Since ungulates tend to move rapidly through sparsely vegetated habitats in pursuit of their daily ration, b will be large unless densely vegetated habitats are either very rare or differ only slightly from the sparse ones. Consequently, $G - B$ will almost always be positive and following of the female by the male should rarely occur. But this brings us to the third condition. Even if $b > a$ the ability of territorial males to garner superior resources must be great for territoriality to be favored since

$$p - p' > \frac{C}{G - B}.$$

And this is not likely to occur if the vegetation is evenly distributed in either a mostly sparse or mostly dense fashion. Thus the more evenly distributed the vegetation the less likely it becomes that territoriality will evolve. The fourth condition for the breakdown of territoriality depends on the absolute value of reproductive gains in the respective habitats. In other words, the adaptive value of territoriality depends on the magnitude of $G - B$. If the number of females likely to be encountered in a good habitat is small, then even if the relative chances of encountering a female and mating with her are much higher in the dense habitat than in the sparse one, $G - B$ will be much smaller than if the same habitat-specific likelihoods of mating apply and females are more abundant. As a result, when females are rare the chances of the left hand side of the equation being larger than the right hand side are small, thus favoring male-following behavior.

In summary, the wandering strategy should replace the territorial one if (1) the costs of territorial defense are high, (2) the vegetation is evenly distributed irrespective of being either a dense carpet or a sparse array of stems, or (3) females are rare. Wandering can take one of two forms, however. If females are widely dispersed, as is likely to be the case if the vegetation is sparsely distributed, then males will most likely only encounter solitary females, and the polygyny that develops will be sequential. If the vegetation is more densely distributed, however, females may be found in groups and if interference competition among females is low associations may be long-lasting. As a result, males may be able to defend harems.

Ecological features of arid environments

Although only a few ungulates inhabit deserts, there are many species with broad ecological ranges that have populations living in arid and semi-desert habitats. Obviously these habitats provide sufficient food and water for populations to persist. But what does the resource base actually look like? And what effect does it have on life history and mating patterns? At least for the semi-desert of Northern Kenya (Samburu Game Reserve) where Grevy's zebra and oryx thrive, rainfall is sparse, averaging less than 300 mm per year. But more important, it is highly unpredictable (Ginsberg, 1988). Although there are usually two rainy periods each year, when they occur is quite variable. In fact, even in months where rainfall during the last 10 years has on average been low, occasional deluges have occurred. Thus even though the amount of precipitation necessary to stimulate plant productivity in deserts is typically low (about 250 mm), the probability that this threshold will be reached in any one area is much lower than in more temperate and mesic habitats. Consequently, it is not too surprising that in arid environments vegetation occurs in patches but is sparsely distributed overall. Moreover, what grass there is grows quickly and rapidly declines in quality as support structures dominate the more nutritious leaves.

Given this resource distribution one would expect overall population densities of desert

animals to be low but at times to increase where aggregations can take advantage of rich ephemeral resources. Moreover, without any predictable period of rapid vegetation growth, one would not expect females to synchronize their births. At least for Grevy's zebra living in Samburu births can occur in almost any month of the year (Ginsberg, 1988). Thus from a male ungulate's perspective in areas where rainfall is unpredictable, receptive females will be sparsely distributed in both space and time. From the mating system model sparse but even distribution of resources and a scarcity of receptive females are conditions favoring the evolution of following strategies. From a female ungulate's perspective sparsely distributed vegetation with occasional widely scattered rich patches should make finding enough food to maintain bodily condition and support reproduction difficult. This should require long daily treks at a brisk pace if daily energy and water requirements are to be met. Possible selection would favor smaller body sizes. But if the weight-specific costs of transport are to be kept low the opposite might be favored. In any event, scramble competition should be intense, and the prospects for infant and juvenile survival should be low, relative to those of adults. Females should graze in a non-selective fashion and, according to life history theory, females should invest in themselves, or heavily in one, or at most a few, offspring.

Broad interspecific comparisons

When East (1984) divided African ungulates into two categories, those inhabiting arid (<700 mm annual rainfall) and moist savannas, a number of patterns emerge that lend some weak support for the predictions of the models (Fig. 2). First, although all the grazing ungulates support Jarman's (1974) principle that small-bodied species must feed selectively on high quality widely dispersed food items (class a and b feeders), whereas large bodied species could subsist by feeding unselectively on more abundant and more evenly distributed low quality forage (class d and e feeders) for a given weight, most arid savanna species were less selective foragers than their moist savanna dwelling counterparts. And since Jarman (1974) has also shown that particular feeding classes correlate with

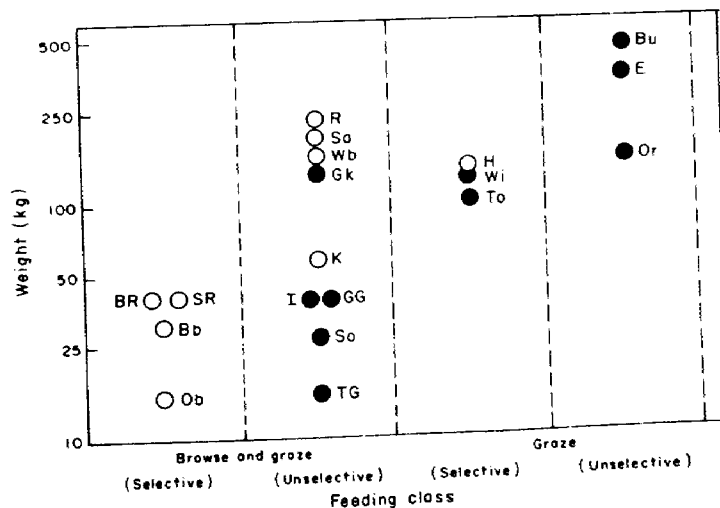


Figure 2. Weights and feeding styles of ungulates classed as arid adapted (●) and mesic (○). Bb, bushback; BR, bohor reedback; Bu, buffalo; E, eland; GG, Grant's gazelle; GK, greater kudu; H, hartebeest; I, impala; K, kob; Ob, Oribi; Or, oryx; R, roan; Sa, sable; Sp, springbok; SR, southern reed back; TG, Thompson's gazelle; To, kopi; Wb, waterback; Wi, wildebeest. Adapted from East (1984).

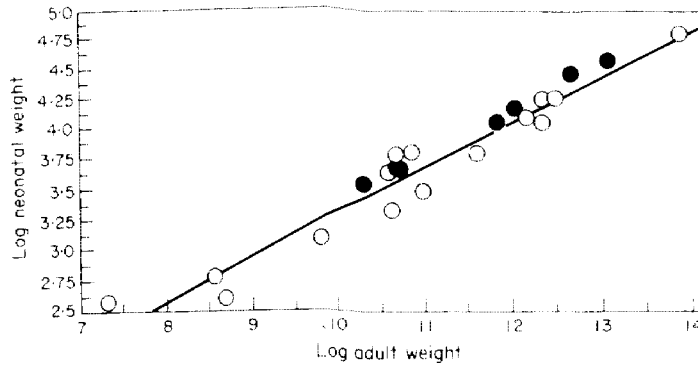


Figure 3. Relationship between adult and neonatal body weight. (●), arid species and (○), mesic species.

particular social systems (feeding class a and b with monogamous territoriality, class c with polygynous male territoriality, and class d and e with polygynous male following), on a weight-specific basis arid forms tend to show more following tendencies than the moist species. It is also interesting to note that for any particular feeding class the arid species are smaller than the moist ones.

Second, the arid species tend to give birth to offspring that are slightly heavier than those of ungulates in general. Figure 3 shows that when the logarithm of birth weight is plotted against the logarithm of maternal weight, the six arid savanna species from East's sample all fall above the regression line. Since all ungulates give birth to precocial young, this result suggests that females living in arid environments where juvenile mortality is relatively high and which give birth to only one youngster at a time are in fact being selected to increase investment in the offspring.

Detailed interspecific comparisons

Although these trends are suggestive, they are based on a limited collection of widely varying species. A stronger determination of what makes the behavioral ecology of arid ungulates special can only come from comparisons among species that are phylogenetically closely related. Similarities and differences that correlate with differences in environments can then be more readily interpreted. Perhaps the best collection of species comprises the equids. There are seven living species, two horses, three zebras, and two asses. All make a living in basically the same way by grazing, and yet they range from the most arid deserts of Ethiopia and Somalia (asses), through the semi-deserts of northern Kenya (Grevy's zebra), to the mesic savannas of eastern, central and southern Africa (plains and mountain zebras). What makes them so fascinating, is that they show a variety of social systems which, as a first approximation, can be divided, as Klingel (1974) was the first to do, into two types. In one, typified by horses, and plains and mountain zebras, females live in permanent membership groups tended by a dominant stallion. In terms of the mating system model these so-called harems are tended by male followers. In the others, females live in open membership groups that wander through large territories (on average 5.8 km², but often 10 km²) defended by solitary males. Interestingly, the territorial systems are in the more arid habitats, whereas the harem or following systems are in the more mesic ones. Are these patterns the result of different ecologies? And if so, do they support the predictions of the mating system model?

In short, the answer to both questions is 'yes'. In the Samburu-Buffalo Springs Game Reserves of northern Kenya both Grevy's and plains zebra live sympatrically, although the latter is at the edge of its range. Both species show the same aseasonal pattern of births

Table 1. Behavioral, ecological and life history attributes of Grevy's and plains zebras

	Grevy's zebra	Plains zebra
Probability of infant surviving to 1 year	0.46	0.21
Inter-drinking interval	1-3 days	1 day
Home range quality (g biomass/m ²)	106 ± 90	300 ± 32
Walking rate while grazing (steps/min)		
dense vegetation	10.9	7.2
sparse vegetation	12.0	—
Female body weight (kg)	330.0	220.0
Day range (km)	14.3	5.2
Home range (km ²)	25.6	8.1
Index of habitat openness*	0.25	0.40
Rate of female aggression (supplants/h)	0.6	0.2

* Bitterlicht method.

illustrated earlier for Grevy's zebra, but as is shown in Table 1, the species differ in a number of important behavioral and ecological ways. First, infant mortality is much higher in the plains as opposed to Grevy's zebra. Second, plains zebras are much more dependent on standing water. All adults drink at least once a day, whereas Grevy's females only drink once a day when lactating. Otherwise, males and females frequent standing water once every 2-3 days. Third, Grevy's zebra can also inhabit areas where vegetation is on average much less abundant but much more variable. In such habitats it is not infrequent to see females take close to 12 steps/min while grazing. And even when both species forage in the same habitats, Grevy's females move much more quickly while foraging than do plains zebra females. Fourth, Grevy's females are also more than 50% heavier than plains zebra females. As a result Grevy's females, presumably because they have to acquire large quantities of sparsely distributed vegetation, move significantly farther during the day than do plains zebra females. And often they do so through dense scrub, something the more open savanna plains zebra rarely has to contend with. It is as if the plains zebra has been selected for enhanced foraging efficiency within any given area or patch, while the Grevy's zebra by virtue of its large size has been selected to maximize travelling efficiency among areas or patches. Both strategies are effective in maximizing foraging success, but because of trade-offs generated by other features of biology each apparently does better in a particular habitat. Lastly, the rate of female-female aggression as measured by supplants while feeding is lower among plains than among Grevy's zebra. When these features are taken together, it becomes clear that Grevy's and plains zebra experience the same environment in different ways. Whereas plains zebra females are fairly sedentary, amicable and form long-lasting cohesive groups, Grevy's zebra females are mobile, wide-ranging, competitive and form opportunistic aggregations that readily fission.

At first glance, it might appear that in both species males should be followers even if for different reasons and with different mating system consequences. For plains zebras food is distributed fairly densely and evenly, and female ranging is limited by dependence on steady supplies of standing water. Under these conditions both $p - p'$ and $G - B$ are small and the model predicts that males should be followers. Since interference competition among females for these densely packed resources is low, living in groups is facilitated. As a result, following males can tend groups of females. For Grevy's females the speed at which they travel and the fairly dispersed nature of the vegetation should also make following the favored strategy since both the values of $p - p'$ and $G - B$ should also be small. However, the distribution of sparse vegetation in the Samburu Game Reserve is *not*

continuously or evenly distributed. Despite the low overall quality of the resource and its sparse distribution, there are regions where it is markedly better and females use these areas preferentially as grazing highways. By defending large areas in these zones males are able to bias the quality of the vegetation they control so that it is much better than that found in an average home range. On average, the proportion of high quality vegetation in a territory (p) is 0.36, whereas the proportion in an equivalently sized home range of bachelor males (p'), which occur in areas where breeding males do not establish territories, is 0.21. As a result $p - p'$ becomes quite large; thus territoriality is in fact favored. Moreover, Grevy's males can keep the costs of defense low by continually communicating with neighbors and by seeking out young males and dominating them, thus reducing the likelihood of their attempting takeovers (Ginsberg, 1988).

Asses live in even more arid environments, where conditions of resource distribution and female movements are even more extreme than those found in Samburu and shown by Grevy's females. Although male asses also typically exhibit territoriality, there is some indication that territoriality is not the only mating strategy. In both Moehlman's (1974) and Woodward's (1979) studies of feral asses, most reproductively active males were followers searching out individual receptive females. From their accounts, it appeared that only those males who could defend areas that controlled access to water, established territories. Thus again, only in areas where $p - p'$ is large does it appear that territoriality is favored. But much more work is needed before this mixture of strategies in asses is substantiated, and the pattern of female movements and associations is driven mostly by the distribution of water and not forage. At least for Grevy's zebra females, water periodically becomes the critical, or controlling, resource. Female wandering and use of long day ranges ceases when they are lactating and their need for water rises markedly (Rubenstein, 1986). Females with newborn foals reside for many months exclusively with one male and confine their movements to the vicinity of his territory. Interestingly, only males that defend territories controlling access to standing water in open areas where predators cannot hide are selected by lactating, and because of post-partum estrus, receptive females (Rubenstein, 1986). So even in the Grevy's zebra there may be a tendency for territoriality to develop when water becomes the most critical resource and access can be economically controlled. It is also interesting to note that when asses inhabit lush continuous grasslands of subtropical coastal islands, males abandon territoriality, and like their plains zebra relatives, become followers, tending harems (Moehlman, 1974).

Intraspecific comparisons

The best means of determining the adaptive value of different life history and mating patterns is to examine different populations of the same species inhabiting different environments. Unfortunately, few ungulates exhibit such a wide geographic range, and of those that do, ecological, life history and mating system data rarely exist for enough populations. Bighorn sheep, Dorcas gazelles, and Oryx are some of the exceptions.

Bighorn sheep range from the alpine areas of Canada to the deserts of the south-western U.S. Perhaps the most striking feature about bighorn life histories is that females in desert populations have significantly longer birthing seasons than do females living in alpine populations (Fig. 4; Bunnell, 1982). The season of the desert populations not only starts earlier but it finishes later. We have already seen that some deserts are characterized by unpredictable rainfall, and that in these areas, timing births so that lactating females are sustained by the best forage, is difficult. Apparently unpredictability, not low levels of rainfall, are responsible for spreading out the desert bighorn lambing period. Even in the alpine populations receiving less than 250 mm of rainfall, the onset of the rains, and thus appearance of new vegetative growth, is highly predictable and as a result even in these alpine populations the first births of the season are timed to occur just at the right time, and do not differ from those populations receiving more copious predictable rainfall. Account-

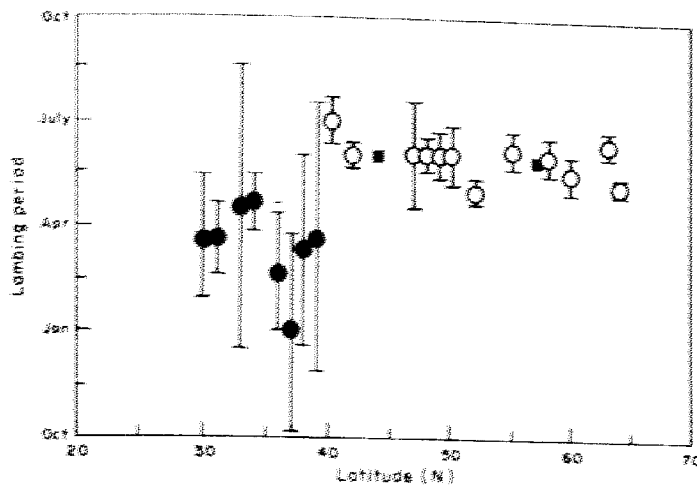


Figure 4. Lambing periods of North American mountain sheep vs. latitude. (●), lambing period—desert; (○) lambing period temperate. Bars depict ranges. Adapted from Bunnell (1982).

ing for abrupt termination of birthing in alpine populations is more problematic, however. Does the season end sharply because there is intense selection for young to attain some critical size before the onset of harsh winter conditions? Or is the end so sudden because all the females have in fact conceived by the end of their second estrus cycle? That all alpine females should become pregnant so quickly while desert females do not could be a function of only alpine populations having well defined lambing areas where males and females are concentrated, and heightened male stimulation hastens the onset of estrus. But deserts also lack harsh winters so it is difficult to determine why desert populations continue to give birth until later in the year.

When it comes to investment in young, desert females invest slightly more than do alpine females (Table 2). Since Berger (1982) showed that the coefficient of variability of offspring success was higher for desert as opposed to alpine populations (Table 2; $p = 0.07$) it appears that as life history theory predicts, when adult survival prospects are relatively high female bighorns invest heavily in their one offspring.

The typical mating system of bighorn sheep involves male following. Individual males search for females inhabiting open membership groups that are about to come into estrus. When males find one they tend her both before and for some time after mating, unless they are displaced sooner by a more dominant male. Then they leave and search for another female. In the one desert bighorn population in which male mating behavior was recorded, Lenarz (1979) found that females travelled in fairly permanent groups and that individual males, who maintained spermatogenesis all year, stayed with them for long periods, one lasting 57 days.

Table 2. Life history characteristics of desert and alpine bighorn sheep

	Birth weight/maternal weight ¹	Coefficient of variability in offspring survival ²
Desert	8.2	37.3
Alpine	7.5 ± 0.03	22.7

¹ From Bunnell (1982).

² From Berger (1982).

Clearly, a variant on the bighorn theme is occurring in this Chihuahuan Desert population. But at this stage it is impossible to determine if these bighorns have bypassed the territorial phase, jumping from one form of following to another. If so, it must be because females are either rare or the vegetation is sufficiently sparse so that $G - B$ or $p - p^0$ are small. Irrespective of which ecological dimension is involved, it is not clear why females in a population of less than 25 individuals should band together more or less permanently instead of spreading out, as is the case even in the more mesic and densely vegetated areas.

This same phenomenon occurs in both oryx and Dorcas gazelles. At least for the oryx, males and females travel in mixed sex herds and males act as followers under normal dry conditions. In wet years males apparently change their behavior and establish territories on ecotones encompassing most of the critical resources females need (Wacher, pers. comm.). Yet in the extremely arid desert of Oman the recently released scimitar horned oryx (a subspecies) travel in groups composed of one male and many females (Stanley-Price, 1986). Again the males are behaving as followers, but in a way that is qualitatively different from when females are more abundant.

By examining the mating system of Dorcas gazelles some insights emerge as to why this pattern of following semi-cohesive groups of females repeatedly occurs in extremely arid areas when female populations are so small. In the southern Negev Desert Dorcas gazelles inhabit a variety of habitats. In some the productivity of the shrubs, bushes, and annual grasses is high, whereas in others it is low. In all habitats the vegetation is sparsely distributed, but it becomes more restricted to smaller and smaller bands in the *wadis* (washes) as productivity declines. Not surprisingly, the density of gazelles declines as productivity diminishes, but as Table 3 shows the social organization also changes. In the highly productive areas where female densities are relatively high males establish territories, but in areas where densities are low males follow small groups of females. These groups change composition occasionally but it appears that males are defending a harem.

Why should this be the case? As illustrated in Table 3, gazelle movement patterns and levels of aggression are influenced by habitat and vegetation quality. In order to forage for the same length of time, gazelles in poor habitats have to cover twice as much ground as those in rich ones. Furthermore, even in large patches the number of aggressive interactions increases dramatically with group size during the driest part of the year which is when the rut occurs. Whereas a female can remain in a 100 m² patch for an average of 16.4 min when in a group of three, a female can only feed for an average of 2.1 min when the group consists of nine females (Baharav, 1982). Although these effects are less extreme in larger patches of vegetation, the average stay time decreases by about 20% for the same increase in group size. As a result, group sizes are small and female movements are rapid in the poorest habitats. These are precisely the conditions under which the model predicts that male ungulates should become followers. Since aggression among females appears to prevent associations of more than three from forming, it is possible that simply because intense competition has already dispersed most females from the habitat, for the few that remain the groups they join (possibly to lower the hazards of predation) become somewhat

Table 3. *Habitat and behavioral characteristics of Dorcas gazelles*

Habitat	Productivity (g dw/m ² /year)	Density (n/km ²)	Female group size	Home distance range covered in 6 h
Acacia woodland	139	5.0	1-2	—
Wide <i>wadi</i> beds	81	2.0	1-2	5 km ²
Narrow <i>wadi</i> beds	40	0.1	2-3	12 km ²

cohesive. When this occurs males apparently benefit. Presumably by following one female a male has a high probability of following a few and an apparent harem forms.

Conclusion

At least for ungulates ecology exerts a strong effect on shaping life histories and systems of mating. As environments change so do the tactics of reproduction for both males and females. And in many instances the changes are in accord with evolutionary theory. Yet as environments, deserts do *not* seem to exert unique effects on behavior. The rules by which females acquire critical resources and invest them in reproductive options, and those by which males compete to acquire access to reproductive females, are the same for animals living in arid and mesic habitats. Thus it is not surprising that among the arid adapted ungulates the same range of mating systems appear as are commonly seen in the more mesic adapted species.

If there are any special patterns in deserts they will be quantitative as opposed to qualitative. Possibly some social and life history variants such as smaller adult body sizes, disproportionate investment in a few robust young, and mating systems based on following as opposed to territoriality will be more common in arid as opposed to mesic climes. Generalizations such as these derived from such a small sample of species must, however, be viewed with caution. At least with respect to body size the Grevy's zebra counters the trend. But does it break the rule, or just underscore the importance of understanding how the *whole* organism is adapted to cope with desert conditions? Certainly physiological and morphological adaptations will be present and serve as constraints. Trade-offs will exist, since being good at one task necessarily means being mediocre at another. When it comes to foraging there are opportunity costs associated with either efficient foraging or travelling. Which strategy is better clearly will depend on environmental conditions, but as Fig. 1 stressed, it will also depend on other pre-adaptations. Thus large size might predispose an individual to one strategy over another because its perceptions of the challenges posed by the environment might be very different from those faced by a smaller sized individual. Since it is likely that different desert-adapted species might perceive the same environment in different ways, no one set of life history or social patterns should appear in desert animals. And perhaps since the pre-adaptations may make the arid environment appear no more stressful to an arid dwelling animal than a mesic habitat is to a mesic dwelling one, the various behavioral responses exhibited by arid forms may match those adopted by the mesic forms.

From an ungulate's perspective, if there is to be one feature of deserts that is special, it must be the availability of water. But even this is not likely to be universally true even among ungulates. Some species such as many gazelles, oryx, and gerenuk can exist without needing to frequent standing water. Only for those species that must acquire water can its extreme patchiness in both space and time potentially lead to a biased set of behavioral outcomes. For example, the needs of females for water may change as their reproductive state changes. Since this might accentuate the differences among sub-populations of females in different receptive states in the ways that they use the environment, the range of male mating strategies used to cope with female movements may be limited. Or alternatively, the unpredictability of water may qualitatively change a population's entire breeding cycle and synchrony. Again, the response by males to these dramatic changes in female patterns may also lead to responses that are qualitatively different from those exhibited by males living in more mesic areas. But if different deserts have different patterns of water availability the particular patterns that emerge in each desert will probably differ. Nonetheless, as we have seen in a limited sample of ungulates, the general rules by which animals respond should be the same. It is the search for these rules, and the specific environmental features as well as the internal constraints that shape an animal's perception of exactly how challenging these environmental features are, that behavioral ecologists working on desert organisms of all types should be focusing on.

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