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Weaning Conflict in Desert and Mountain Bighorn Sheep (*Ovis canadensis*): An Ecological Interpretation

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With 4 figures

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Abstract

Field data on weaning behavior in bighorn sheep (*Ovis canadensis*) were collected from populations in British Columbia, southern California, and one transplanted from the original B.C. study site to eastern Oregon. These areas were designated mountain, desert, and transplant, respectively. Seasons that were energetically stressful to lactating ewes were predicted. Summers were implicated for desert ewes; winters for ewes in colder and more seasonal northern environments. Although the temporal distribution of milk available to lambs varied between the three study populations, ewes generally weaned their lambs prior to the onset of the predicted stressful periods. In the desert, weaning occurred more abruptly than it did in the two more northern populations. The evolution of weaning strategies is discussed in subspecies of bighorn sheep based on proximate and ultimate factors.

Introduction

One of the tasks confronting ethologists is to explain the observed diversity of behavior in natural unmanipulated populations in terms of selection pressures (Fisher 1930; Alexander 1974). Such an evolutionary approach has been widely stressed in recent reviews of behavioral phenomena (Alcock 1975; Brown 1975; Gould 1977; Tinbergen 1965; Wilson 1975). This approach has been applied to the weaning process (Reiter et al. 1978; Trivers 1972, 1974). Classically, weaning has been thought of as a gradual process through which parous mammals decrease the dependence of their offspring on milk (Brown 1959; Harper 1970). It is a slow process involving maternal aggressive acts ranging from subtle signals (see Lent 1974) to active fighting and hostility (Altmann 1958; Eisenberg 1966).

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In a set of very stimulating articles, TRIVERS (1972, 1974; see also MAYNARD SMITH 1976) theorized about the contrasting ways in which natural selection operates on fitness in successive generations (e.g. parent-offspring conflict). He reasoned that a point in time is reached when a mother decreases the amount of energy invested in current offspring and reinvests it in future offspring, the major proximate result being a decrease in milk production to current progeny. Hence, these progeny are faced with a dwindling resource base and they turn elsewhere to alleviate hunger (i.e. grazing in infant ungulates). This process is termed *weaning conflict* because of the contrasting interests of the mother and offspring.

Although in theory TRIVERS' (1974) model appears heuristically valid, there are few data available on which to interpret its applicability. It would prove most interesting to determine how much energy (inferred through milk production) mothers allocate to postpartum offspring, at what stages (age) young are weaned, and if different strategies for weaning exist between mothers exposed to different ecological conditions.

Studies of milk consumption, lactation, and weaning have been performed in a wide array of captive and natural settings. Recently, REITER et al. (1978) studied differences in the behavior and weaning strategies of young male and female elephant seals and related them to the evolution of pinniped mating systems. However, many prior works have concentrated on proximate factors affecting the behaviors of both mother and young and they were unable to infer energy budgets by providing quantitative information. Data are available that quantitatively describe postpartum events for domestic ungulates, especially sheep (*Ovis aries*) (EWEBANK 1964; MUNRO 1962; WALLACE 1948). Such data have been used by GEIST (1971), HOREJSI (1976), and SHACKLETON (1973) to examine and predict the relationships that occur between the environment and weaning in wild populations of bighorn sheep (*O. canadensis*). In this paper I consider weaning conflict in natural populations of bighorn sheep from desert and northern environments and examine the hypothesis that parous ewes exposed to contrasting environmental conditions will utilize different strategies to wean their offspring. Specifically, I provide an ecological interpretation for the behaviors involved in weaning through the consideration of proximate and ultimate factors.

Methods

1. Study Areas

The first study site was located in the Chilcotin-Cariboo of the central interior of British Columbia, Canada. The habitat occupies the northern limit of grassland in North America and it was centered at the confluence of the Chilcotin and Fraser Rivers (see DEMARCHI and MITCHELL 1973 for a more detailed description). The population size of California bighorn sheep (*O. c. californiana*) in this area is about 400 (MITCHELL unpubl.). Data were collected from May through November 1976.

The second study site was located in the Santa Rosa Mountains, an arid insular range in southern California. These mountains represent the westernmost extension of the Colorado Desert (JAEGER 1957). Rainfall is scant (about 90 mm annually) and the vegetation is primarily creosote scrub (TING and JENNINGS 1976). The population size of peninsular (also called desert) bighorn sheep (*O. c. cremnobates*) is estimated at 250. Data were collected from January through April 1977. Further details of the habitats and population may be found in BLONG and POLLARD (1968), TURNER (1973), and TING and JENNINGS (1976).

The third study site was located at Hart Mountain, a massive fault block in the Great Basin Desert of eastern Oregon (see Fig. 1). California bighorn sheep were transplanted from the original Chilcotin study site to Hart Mountain in 1954. The vegetation is characterized by *Artemisia* scrub associations. I observed this last population from May through July 1977.

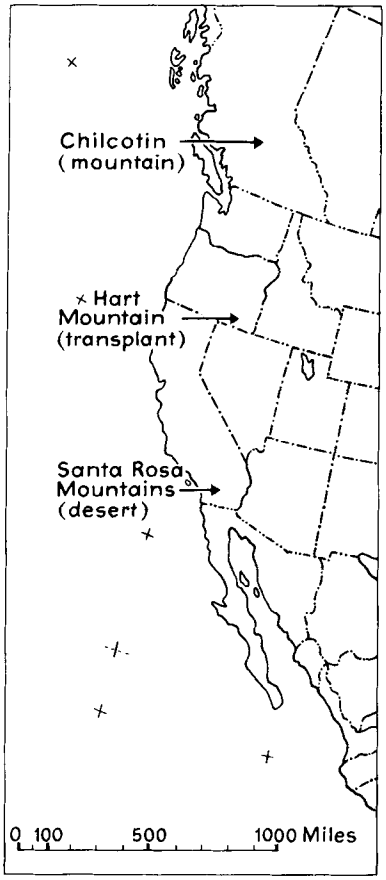

Fig. 1: Map showing the geographical locations of the study sites

Further details of the habitat, sheep population, and its history are found in KORNET (1978). The population size is estimated at 200 (KORNET 1978).

For simplicity, I shall call sheep from the northern environment "Chilcotin" or "mountain" sheep (although I realize mountain sheep refers to a number of subspecies including O. *c. canadensis*). Likewise, I shall call peninsular bighorns "desert" sheep, and sheep from Hart Mountain "transplants".

2. Data Collection

Data on mother-infant relationships were collected by stalking sheep in the field almost daily. Observations were made at all hours of the day and were aided by the use of binoculars and spotting scropes. Sheep were observed in the Chilcotin for 896 h, at Hart Mountain for 293 h, and in the desert for 454 h. Data were either recorded directly into a cassette tape deck or written onto note cards. Only data from undisturbed sheep (unaware of my presence) were used. Ages of lambs were estimated visually by their size in relation to ewes. Since there are no data on their body sizes, these judgements were based on my prior experience with lambs of known ages at the Okanogan Game Farm, British Columbia and my personal experience with captive lambs and my own desert lamb.

3. Definitions, Assumptions, and Interpretations

Suckling behaviors refer to those acts important in the acquisition of milk by lambs, whereas nursing activities are milk-related behaviors performed by ewes (COWIE et al. 1951; HOREJSI 1976). The behaviors quantified during this study are defined below.

1. Suckling bout: The duration of time during which lambs pull on or are in contact with the udder. Suckling bouts are considered successful suckles (e.g. milk is obtained) and were timed to the nearest second.
2. Suckling rebuff: A lamb unsuccessful at obtaining milk. Rebuffs were recorded when lambs 'obviously' tried to grasp the nipples or approached the udder.
3. Rejection: Ewes not permitting lambs to suckle. Rejections were recorded when lambs approached ewes and were not permitted access to the udder. During rejections, ewes lifted their legs, walked away, or butted lambs.
4. Cheating: Lambs attempting to suckle from mothers other than their own.
5. Suckling rate: Frequency of lamb suckling per h of ewe activity. Ewe activity is defined as time spent available for suckling. Ewes were considered available any time they were not lying.

Some of the above definitions may be explained from proximate (immediate) or ultimate (evolutionary) perspectives. My interpretations of these

perspectives are provided below. Also discussed are assumptions regarding suckling success and milk consumption.

Duration of Suckling Bout. With all other factors being equal, lambs that suckle longer obtain more milk (BROWN 1964; FLETCHER 1971; HOREJSI 1976; MUNRO 1962). Ewes that nurse lambs for longer durations have more milk in their udders. A lamb may try to suckle but should its mother have no available milk, the lamb cannot benefit. A lamb has no choice in the matter. The available milk is limited by the mother.

Suckling Rebuff. It is assumed that a lamb is not satiated when it attempts to suckle but is rebuffed. However, if a lamb does not attempt to suckle it does not necessarily mean that it is satiated. Perhaps a lamb learns that no milk is available so it does not attempt to suckle and it may not be rebuffed. But, if a lamb terminates a bout it probably is satiated. A lamb will enhance its survival by suckling often or long (see BROWN 1959; EWEBANK 1967; FLETCHER 1971; GEIST 1971; HOREJSI 1976; MUNRO 1962; SHACKLETON 1973).

Rejection. A ewe that has no milk available will reject lambs. Udders without milk may be painful if they are sucked upon, which could be another reason why rejections occur (GEIST 1971). A bout of suckling is probably terminated when milk is no longer available. Ewes may reject lambs for two reasons (that could be interpreted proximately or ultimately). (I) Ewes most likely attain a point where no further energy demands will be tolerated. Hence, the benefit/cost ratio (TRIVERS 1974, 251) is low. Rather than further invest energy into current offspring, weaning occurs and positive body growth (weight gain) ensues in ewes. Later this energy may be reinvested into future offspring. (II) Rather than abruptly terminating maternal investment by ceasing nursing activities, a ewe may encourage her offspring to engage in alternative forms of energy acquisition) (i.e. grazing). The difference between (I) and (II) is that (I) is a rapid process whereby the ewe ceases abruptly any form of assistance and reinvests in future offspring. In (II) weaning is gradual as the ewe still allocates some energy to current offspring. Although (I) and (II) are conceptually different, they represent end points of a continuum (BARNICOAT et al. 1956; BROWN 1959, 1964; ESPMARK 1971; EWEBANK 1964, 1967; GEIST 1971; GRAHAM and SEARLE 1970; HODGE 1966; HOREJSI 1976; JOYCE and RATTRAY 1970; MOORE 1966; MUNRO 1962; SHACKLETON 1973; SPEDDING 1965).

% Suckling Success. % success equals the number of suckles (bouts) divided by the number of rebuffs plus the number of suckles. If ewes have sufficient milk, lambs will not be rejected (see above). % suckling success is a measure of an ewe's tendency to provide milk in response to the demands of lambs. As % success decreases, the maternal benefit/cost ratio decreases. At some point then, (I) or (II) apply (see BROWN 1959, 1964; ESPMARK 1971; EWEBANK 1967; FLETCHER 1971; FORBES 1969; GEIST 1971; HODGE 1966; JOYCE and RATTRAY 1970; SHACKLETON 1973; SPEDDING 1965; TYLER 1972).

Milk Consumption. Many factors (i.e. rate of milk production, sucking power of lambs, etc.; see Fig. 2) affect how much milk is consumed. Field data generally preclude quantifying many of these variables. I have therefore selected two of the more simplistic and easily quantifiable variables to estimate milk consumption. Milk consumption equals duration times suckling rate. With all other factors being equal, lambs that suckle more

frequently and for longer durations consume more milk. This interpretation has been widely accepted (BROWN 1959, 1964; GRAHAM and SEARLE 1970; MUNRO 1962; see also HOREJSI 1976) but several alternatives exist. The following questions may be asked: Why do some lambs suckle more frequently than others? One alternative (III) is that lambs are rewarded with milk, therefore they return more often to suckle, and consequently they become heavier. Another alternative (IV) is that lambs are hungry, therefore they return more to suckle. The difference between (III) and (IV) is only one of degree. For instance, consider a lamb that is not rewarded as fully as the next. It may be slightly lighter because it has not received as much milk. Consequently it returns more often to suckle (or it attempts to suckle). An alternative to (III) may be that lambs do not return to suckle often because they are unrewarded (negative reinforcement). Hence, their ewes have no available milk. If this is the case, the ewe again is ultimately controlling the energy available to its offspring and (I) or (II) apply.

Results

1. Factors Influencing Weaning Age

Fig. 2 is a flow diagram summarizing the major proximate factors that affect the age(s) of weaning in lambs. It is based mainly on studies of domestic

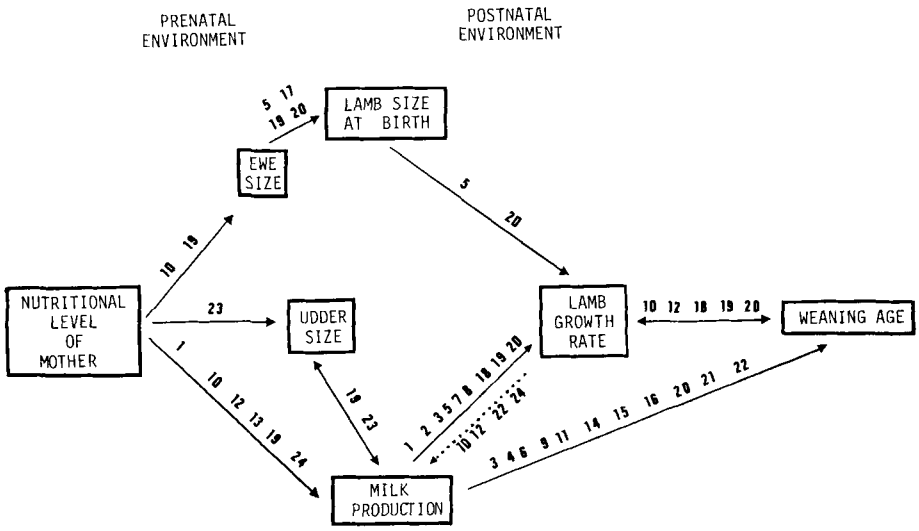

Fig. 2: Flow diagram of factors affecting lamb growth rates and weaning ages. Numbers refer to the following references: 1 — ARMAN et al. (1974); 2 — BARNICOAT et al. (1956); 3 — BROWN (1959); 4 — BROWN (1964); 5 — BUTTERWORTH and BLORE (1969); 6 — ESPMARK (1971); 7 — EWEBANK (1964); 8 — EWEBANK (1967); 9 — FLETCHER (1971); 10 — FORBES (1969); 11 — GEIST (1971); 12 — GRAHAM and SEARLE (1970); 13 — HAFEZ and LINEWEAVER (1968); 14 — HODGE (1966); 15 — HOREJSI (1969); 16 — JOYCE and RATTRAY (1970); 17 — MILLAR (1977); 18 — MOORE (1966); 19 — MUNRO (1962); 20 — PEART et al. (1975); 21 — SHACKLETON (1973); 22 — SPEDDING (1965); 23 — THOMSON and THOMSON (1953); 24 — WALLACE (1948). Ewe size, udder size, milk production, and lamb size at birth are located between the pre- and postnatal environments since all are affected by these environments

sheep although several studies are incorporated from wild species. The major points are: (1) pre- and especially postpartum nutrition affects the amount and quality of milk produced; (2) pre- and postnatal nutrition affects ages at weaning; (3) milk production influences lamb growth more than the converse relationship (hence, the dotted arrow). The rationale behind this arrangement is that: (i) ewes must produce milk if lambs are to grow; (ii) ewes continue to produce milk (and do not 'dry up') immediately after lambs die; and (iii) lamb growth rate affects age at weaning although most agricultural studies have concentrated on the relationships between milk production and weaning age. These studies, primarily of domestic sheep, indicate that ewes raised on better quality diets produce more milk for their offspring which are then weaned at a later age, and are heavier than lambs reared by ewes that are not as well fed (see also GEIST 1978).

2. Suckling Duration, Frequency, and Success

The mean duration of suckling bouts for lambs at various ages is illustrated in Fig. 3. At all ages desert lambs suckled the longest. They, in turn, were followed by transplant lambs, while mountain lambs suckled for the shortest durations. The number of different lambs on which these data are based are: desert N = 31; transplant N = c. 70; mountain N = c. 130.

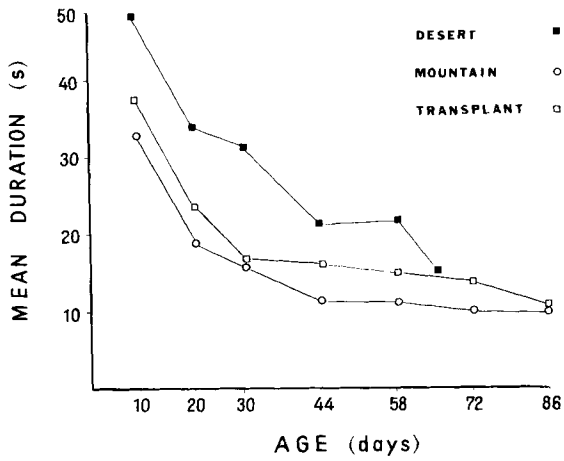

Fig. 3: The relationships between duration of suckling bouts and ages of lambs in several populations of bighorn sheep. Desert N = 172; Mountain N = 341; Transplant N = 226

Since the duration of suckling bouts in itself generates no meaningful indication of milk consumption (HOREJSI 1976), I considered suckling rate in conjunction with duration (see Methods). For one to 10-day-old lambs in the desert, transplant, and mountain populations mean suckling rates were 2.64, 1.50, and 0.44 bouts/h individual, respectively. At this age, the difference in suckling rates between desert and mountain lambs was significant ($t = 3.64$; $p < 0.01$). After this age, however, no significant differences in suckling rate occurred between the three populations ($F = .795$; $df = 2, 26$; $p < 0.463$).

Average total milk consumption (duration × frequency; see Methods) for 65-day-old lambs was greatest in the desert (296 milk units), intermediate in the transplant (161 milk units), and least in the Chilcotin (130 milk units). In fact, milk consumption units for the Chilcotin and transplant lambs at 86 days of age (160 and 195, respectively) were still far below those of desert lambs at 65 days of age, the time at which I departed from the desert study site.

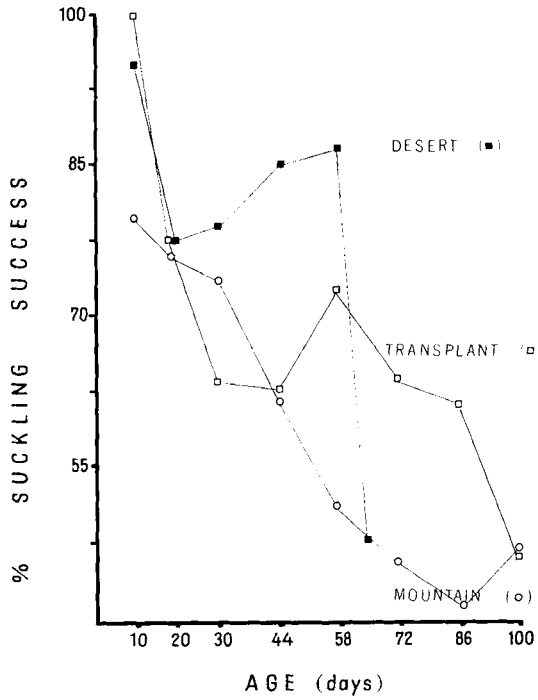

Fig. 4: Age distribution of % suckling success in several populations of bighorn sheep. Sample sizes represent the sum of rebuffs plus bouts; Desert N = 232; Mountain N = 569; Transplant N = 361

The relationship between suckling success and age is shown for the study populations in Fig. 4. It appears that maternal rejections occurred more gradually in the transplanted and Chilcotin populations than in the desert. In fact, in a one week time span (lambs were approximately 58—65 days old) % suckling success in the desert dropped from 87% to 48%.

3. Weaning and Cheating

The rate at which weaning occurred was examined in each population. Most (over 80%) of the successful suckles (e.g. timed bouts) occurred later in the desert (by 35 days of age) than in the transplant or mountain lambs (20 and 10 days, respectively). The number of bouts and rebuffs were standardized by considering them for only the first 65 days of lamb ages in each environment.

Cheating occurred more often in Chilcotin lambs than in the desert or transplant lambs (N = 63, 0, and 1, respectively). Conversely, desert lambs terminated suckling bouts voluntarily more often than lambs from the transplant or mountain populations (N = 18, 1, and 0, respectively) suggesting that they were satiated more of the time (see Methods).

Discussion

1. Field Studies, Problems, and Milk Quality

A shortcoming of the prior field studies of bighorn sheep as well as the present one is the assumption that milk quality varies little between populations. Studies of captive ungulates have demonstrated that not only does milk quality vary with diet (e.g. ARMAN et al. 1974; HAFEZ and LINEWEAVER 1968) but that it also changes with age (MUELLER and SADLIER 1977). Similar data should also be collected for wild populations so that the range of milk quality variability and its effect on weight gain in young animals (see ROBBINS and MOEN 1975) may be assessed for bighorn sheep. Almost certainly, ewes exposed

to food items varying in water content (e.g. desert versus mountain plants) will produce milk differing in composition. Although field studies have been unable to provide detailed and quantifiable data on milk content, they are advantageous because they provide information on the ecological conditions that affect behavioral (i.e. weaning) and demographic parameters.

2. Milk Production and Population Quality

Presently, both the more basic and applied studies of weaning (GEIST 1971; TRIVERS 1974; Fig. 2 and references therein) predict that mothers producing large amounts of milk at little self cost will also raise larger offspring, that grow more rapidly, and are weaned later. In short, such offspring have better chances to escape mortality. Prior studies of bighorn sheep (HOREJSI 1976; SHACKLETON 1973) have supported this idea by providing data that this 'type of lamb' suffers lower mortality; an idea favored in GEIST's (1971) concept of population quality. This concept predicts that the bioenergetic regime available to a population will be reflected in the behavior of its individuals. Populations faced with an abundance of food resources are designated 'high quality' and are characterized by: (1) large bodied and fast growing ewes and lambs; (2) high lamb survival; (3) lambs suckling for long periods of time and playing frequently; and (4) a high intrinsic rate of growth. The reverse conditions are exhibited by low quality populations. Recently, GUINESS et al. (1978a) elucidated the complex network of factors affecting survival in red deer fawns (*Cervus elaphus*).

3. Weaning in Different Environments

The predictions of population quality have been supported by studies that concentrated on geographically separated populations and also one that was studied for several years. SHACKLETON (1973) studied bighorns in Kootenay and Banff National Parks in the Rocky Mountains of Canada, whereas HOREJSI (1976) studied a single population in the Sheep River Valley of Alberta in three different years. GEIST (1971) studied sheep in the Cassiar Mountains, British Columbia, and at Banff. The above studies were broadly similar, in that each involved populations in a mesic, strongly seasonal, and cold environment.

My data on sheep from a more xeric environment indicate that the concept of population quality and classical theory (as presented in Fig. 2) initially does not appear valid. I have observed the opposite relationship. That is, desert lambs on the average were weaned at younger ages and consumed more milk than lambs from the other two study populations. Additional inferential evidence suggests that desert ewes channeled more energy to milk production at earlier postpartum ages than ewes from the Chilcotin or transplanted population. Such evidence was based on the fact that desert sheep are smaller in body size than sheep from the other two populations (ALDOUS et al. 1958; GEIST 1971; RUSSO 1956) and most likely a concomitant reduction in lamb birth size and weight occurs (as it does in domestic sheep: see BUTTERWORTH and BLORE 1969; FORBES 1969; MUNRO 1962). Lambs in the mountains are usually born at about 3.5—4 kg under captive conditions (GEIST 1971; BLUNT et al. 1977). In contrast, desert lambs weigh about 2.3—2.8 kg at birth in captivity (BERGER unpubl.). Since lamb size at birth influences growth rates (Fig. 2) and larger lambs may have relatively greater energy requirements due to faster

growth rates, it seems that desert ewes (which are smaller) must have produced relatively more milk than ewes from the other two study populations.

The apparent differences between milk consumption between populations pose several interesting problems. For instance, why should desert ewes produce a relatively large supply of milk at young postpartum ages and allow lambs greater access to it than ewes from the other environments? What advantages from a Darwinian fitness standpoint may be gained by desert ewes that wean their lambs early?

4. Ecological Differences: Proximate and Ultimate Factors

In order to suggest answers to these questions an analysis of parturition seasons in each study population is necessary. In the Chilcotin, births are synchronized and occur primarily during May. Annual variability in the parturition season is almost certainly small, as it is in other species of ungulates inhabiting seasonal, temperate environments (GUINESS et al. 1978b; SADLIER 1969). In the transplant, births occur in April—May and, again, variability is probably small (KORNET 1978). However, in the Santa Rosa Mountains the parturition season is more variable (BLEICH unpubl.). HANSEN (1965) stated that in the desert, lambs may be born at any time of the year. In other arid ecosystems, some species of ungulates may also undergo births throughout the year (e.g. SEKULIC 1978). During the year I studied sheep in the Santa Rosa Mountains most births were synchronized and occurred during February and March, probably in response to an offseason tropical storm that occurred 5 1/2 months earlier.

I suggest three possible explanations for early weaning in desert lambs from the Santa Rosa population. Future researchers will undoubtedly have greater opportunities for the collection of additional data regarding these possibilities.

First, desert ewes may have evolved a mechanism allowing for rapid weaning. The deserts of southern California are characterized by highly predictable, hot (temperatures may exceed 50 °C), and arid summers. During the summer and fall sheep gather at springs and restrict their movements to within 1—2.5 km of these waters (SIMMONS 1969; TURNER 1973; WELLES and WELLES 1961). As a result these areas tend to be heavily overgrazed. This season represents a stressful period (BLONG and POLLARD 1968; TURNER 1973). During these periods the amount of available quality (e.g. choice) food diminishes and, consequently, ewes in poor(er) physical condition produce less milk (see Fig. 2 and references therein). It thus appears that desert ewes may have evolved a temporal mechanism of energy partitioning. Such an adaptation would consist of allocating large amounts of energy (in the form of milk production) early in the lives of their postpartum offspring (Figs. 3 and 4). Concomitantly, lambs are then weaned at a young age and prior to the onset of the stressful summer.

A second suggestion: perhaps lambs must attain a minimum body weight (or size) before survival is possible. In the deserts, ewes appeared to channel considerable energy into milk production, and the time until lambs attained this weight (or size) may consequently be reduced. After weaning (and during the summer) ewes may then attempt to recover from energetic stresses imposed upon them by their lambs so that investment in future offspring (i.e. reproductive value) is possible (see TRIVERS 1974). If the alternative strategy were adopted and lactation continued throughout the summer, energetic stresses could become too severe, thus jeopardizing any future investment in offspring.

In contrast to the desert, weaning conflict in the transplant or Chilcotin populations may be explained as follows. Selection has not intensively favored ewes that wean early because postpartum periods (summer and fall) are not nearly as stressful as postpartum periods in the desert (see BLONG and POLLARD 1968; TURNER 1973). In fact, it may be adaptive for ewes in the Chilcotin and transplant to prolong nursing so that their offspring attain greater body weights and, thus, improve their probabilities of survival during cold (hence, energetically stressful; STELFOX 1974) winters. In these and other similar environments (for instance, the northern habitats where prior studies have focused) weaning apparently follows classical theory (Fig. 2). That is, lambs are weaned at the oldest ages possible (GEIST 1971, 254; SHACKLETON 1973; HOREJSI 1976).

5. An alternative Explanation

The explanations offered above for inter-regional differences in weaning assume primarily genetic bases evolving as the results of selection pressures in contrasting environments. However, a third explanation also accounts for inter-regional differences. Lambs in the desert may have been weaned abruptly (see Fig. 4) due to changes in food accessibility to ewes or due to changes in the chemical compositions of food items. The time period for which I documented rapid weaning coincided with increasing ambient temperature in the spring. In the desert, this results in wilting, leaching, and dormancy in plants with coincident changes in their water and mineral content. HEBERT (1973; see also MCLEAN and TISDALE 1960; WATKINS 1943) documented chemical changes, especially in protein composition and crude fiber, in natural food items that were growing older in the diets of bighorn sheep. In turn, plants of less nutritional value (or the reduced availability of food) result in decreased milk production in domestic sheep (WALLACE 1948). It seems reasonable then, that during the late spring of the present study, desert ewes became energetically stressed to the point where it no longer benefitted them to produce milk.

BROWN (1959) described the relationship between weaning age and later susceptibility to disease in domestic sheep. He found that lambs weaned early in life were not only in poorer physical condition but they also suffered greater parasitic problems than lambs weaned at a later age. These data are most intriguing when interpreted from an ecological perspective and applied to bighorn sheep.

A trade-off (cost/benefit) in maternal investment may be envisioned. The apparent risk (or cost) to a ewe is that her offspring may suffer reduced chances for survival due to lowered disease resistance if she weans it early. Yet, the benefit to her is the reinvestment into future offspring that survive and reproduce. BLEICH (pers. comm.) suspected epizootic disease as the major factor accounting for the mere 5% survival of 6-month-old lambs at my desert study site. It seems that early weaning of the desert lambs of the Santa Rosa Mountains may have rendered them more susceptible to disease. These lambs obviously did not survive as well as lambs from the other two populations (approximately 80% of the 6-month-old lambs remained in these sites; BERGER unpubl.). Therefore, if an early weaning strategy has not evolved in desert sheep and the abrupt curtailment of milk to desert lambs occurred due to nutrition-related factors or disease, my data do indeed support GEIST's (1971) concept of population quality. The evidence is based on the fact that lambs weaned early also survived poorly in the Santa Rosa Mountains.

During some years, there must certainly be a relationship between energy channeled into milk production (hence neonate weight gain) and later chances of lamb survival. At the ultimate level this may be viewed as a trade-off between maternal cost in terms of reproductive effort during a given year and benefit in terms of 'inclusive fitness' effects (HAMILTON 1964) either in that or subsequent years (e.g. reproductive potential [WILLIAMS 1966; WILSON 1975]).

Summary

Suckling behaviors were studied in three natural populations of bighorn sheep (*Ovis canadensis*). Various aspects of weaning were examined and, based on data from studies of domestic sheep, then applied to bighorns. Ewes in a desert environment (southern California) allocated more energy to milk production than did ewes from populations in more northern environments (British Columbia and eastern Oregon; the latter being the site of a portion of the B.C. population that was transplanted 25 years ago). Ewes from the desert environment weaned lambs more abruptly and prior to the onset of the hot arid summer.

It was suggested that ewes in the desert utilized early weaning as an adaptive strategy to combat the increased energetic costs should lactation have continued through the summer. There appeared to be a trade-off, however, between age at weaning and lamb physical condition. Lambs weaned early appeared to be in poor physical condition. The 'decision' for early weaning in the desert was apparently a poor one from a Darwinian fitness standpoint, as lamb mortality was estimated at 95 %. The reproductive value and ages of individual ewes were unknown. Assumptions and alternative explanation are discussed for the observed inter-regional differences in rates of weaning.

Zusammenfassung

An drei natürlichen Populationen des Dickhornschafes wurde das Säugeverhalten untersucht, und zwar besonders im Hinblick auf die Entwöhnung. In der Wüstengegend Südkaliforniens wendeten die Mütter mehr Energie für die Milchproduktion auf und entwöhnten die Lämmer abrupter vor Beginn des heißen Sommers — beides im Vergleich zu nördlicheren Populationen in British Columbia und Oregon.

Wenn Mütter im Trockengebiet früh entwöhnen, um Kosten der Milchproduktion zu sparen, ist das ungünstig vom Fitness-Gesichtspunkt. Die entwöhnten Lämmer sind in schlechtem Zustand, ihre Mortalität liegt bei 95 %. Alter und Fortpflanzungs-Chancen der Mütter waren freilich unbekannt. Annahmen und Alternativerklärungen zum beobachteten regionalen Unterschied im Entwöhnen werden erörtert.

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Literature cited

ALCOCK, J. (1975): Animal Behavior; an Evolutionary Approach. Sinauer Associates, Sunderland • ALDOUS, M. C., F. C. CRAIGHEAD and G. A. DEVAN (1958): Some weights and measurements of desert bighorn sheep (*Ovis canadensis nelsoni*). J. Wildl. Mgmt. **22**, 444—445 • ALEXANDER, R. D. (1974): The evolution of social behavior. Ann. Rev. Ecol. Syst. **5**, 325—383 • ALTMANN, M. (1958): Social integration of the moose calf. Anim. Behav. **6**, 155—159 • ARMAN, P., R. N. B. KAY, E. D. GOODALL and G. M. SHARMAN (1974): The composition and yield of milk from captive red deer (*Cervus elaphus* L.). J. Repro. Fert. **37**, 67—84.

BARNICOAT, C. R., P. F. MURRAY, E. M. ROBERTS and G. S. WILSON (1956): Milk secretion studies with New Zealand Romney ewes. Pts. V—VI. J. Agril. Sci., Camb. **48**, 9—35 • BLONG, B., and W. POLLARD (1968): Summer water requirements of desert bighorn sheep in the Santa Rosa Mountains, California. Calif. Dept. Fish Game **54**, 289—296 • BLUNT, F. M., H. A. DAWSON and E. T. THORNE (1977): Birth weights and gestation in a captive Rocky Mountain bighorn sheep. J. Mammal. **58**, 106 • BROWN, J. L. (1975): The Evolution of Behavior W. W. Norton, New York • BROWN, T. H. (1959): Parasitism in the ewe and the lamb. J. Brit. Grass. Soc. **14**, 216—220 • BROWN, T. H. (1964): The early weaning of lambs. J. Agril. Soc. **14**, 191—204 • BUTTERWORTH, M. H., and T. W. D. BLORE (1969): The lactation of Persian Blackhead ewes and the growth of lambs. J. Agril. Sci. **73**, 133—137.

COWIE, A. T., S. J. FOLLEY, B. A. CROSS, G. W. HARRIS, D. JACOBSOHN and K. C. RICHARDSON (1951): Terminology for use in lactational physiology. Nature **4271**, 421.

DEMARCHI, D. A., and H. B. MITCHELL (1973): The Chilcotin River bighorn population. Can. Field Nat. **87**, 433—454.

EISENBERG, J. F. (1966): The social organization of mammals. Handb., Zool. **8**, 1—92 • ESPMARK, Y. (1971): Mother-young relationship and the ontogeny of behavior in reindeer (*Rangifer tarandus* L.). Z. Tierpsychol. **29**, 42—81 • EWEBANK, R. (1964): Observations of the suckling habits of twin lambs. Anim. Behav. **12**, 34—37 • EWEBANK, R. (1967): Nursing and suckling behavior amongst Clun Forest ewes and lambs. Anim. Behav. **15**, 251—258.

FISHER, R. A. (1930): The Genetical Theory of Natural Selection. Clarendon Press, Oxford • FLETCHER, I. C. (1971): Relationships between frequency of suckling, lamb growth, and postpartum oestrus behaviour in ewes. Anim. Behav. **19**, 108—111 • FORBES, J. M. (1969): A note on the voluntary intake of lactating ewes, their milk yield, and the growth rates of their lambs. Anim. Prod. **11**, 263—266.

GEIST, V. (1971): Mountain Sheep. Univ. Chicago Press, Chicago • GEIST, V. (1978): Life Strategies, Human Evolution, Environmental Design: Towards a Theory of Health. Springer-Verlag, New York • GOULD, S. J. (1977): Ontogeny and Phylogeny. Harvard Univ. Press, Cambridge • GRAHAM, M. McC., and T. W. SEARLE (1970): Energetic efficiency of lambs and weaners. Austr. Soc. Anim. Prod. **8**, 263—266 • GUINESS, F. E., T. H. CLUTTON-BROCK and S. D. ALBON (1978a): Factors affecting calf mortality in red deer (*Cervus elaphus*). J. Anim. Ecol. **47**, 817—833 • GUINESS, F. E., R. M. GIBSON and T. H. CLUTTON-BROCK (1978b): Calving times of red deer (*Cervus elephus*) on Rhum. J. Zool., Lond. **185**, 105—114.

HAFEZ, E. S. E., and J. A. LINEWEAVER (1968): Suckling behavior in natural and artificially fed neonate calves. Z. Tierpsychol. **25**, 187—198 • HAMILTON, W. D. (1964): The genetical theory of social behaviour. I and II. J. Theor. Biol. **7**, 1—52 • HANSEN, C. (1965): Growth and development of desert bighorn sheep. J. Wildl. Mgmt. **29**, 387—391 • HARPER, L. V. (1970): Ontogenetic and phylogenetic functions of the parent-offspring relationship in mammals. Adv. Study Anim. Behav. **3**, 75—117 • HEBERT, D. M. (1973): Altitudinal migration as a factor in the nutrition of bighorn sheep. Unpubl. Ph.D. diss., Univ. British Columbia, Vancouver • HODGE, R. W. (1966): The relative pasture intake of grazing lambs at two levels of milk intake. Austr. J. Exp. Agril. Anim. Hus. **6**, 314—316 • HOREJSI, B. L. (1976): Suckling and feeding behavior in relation to lamb survival in bighorn sheep (*Ovis canadensis canadensis* Shaw). Unpubl. Ph.D. diss., Univ. Calgary, Calgary.

JAEGER, E. C. (1957): The North American Deserts. Stanford Univ. Press, Stanford • JOYCE, J. P., and P. V. RATTRAY (1970): The intake and utilization of milk and grass by lambs. Proc. New Zealand Soc. Anim. Prod. **30**, 94—105.

KORNET, C. (1978): Status and habitat use of bighorn sheep on Hart Mountain, Oregon. Unpubl. Master's thesis, Oregon St. Univ., Corvallis.

LENT, P. C. (1974): Mother-infant relationships in ungulates. In: The Behaviour of Ungulates and its Relationship to Management. (GEIST, V., and F. WALTHER, eds.) IUCN, Morges, **24**, 14—55.

MAYNARD SMITH, J. (1976): Parental investment: a prospective analysis. Anim. Behav. **25**, 1—9 • MCLEAN, A., and E. W. TISDALE (1960): Chemical composition of native forage plants in British Columbia in relation to grazing practices. Can. J. Plant Sci. **40**, 405—423 • MILLAR, J. S. (1977): Adaptive features of mammalian reproduction. Evolution **31**, 370—386 • MOORE, R. W. (1966): Genetic factors affecting the milk intake of lambs. Austr. J. Agril. Res. **17**, 191—199 • MUELLER, C. C., and R. M. F. S. SADLIER (1977): Changes in the nutrient composition of milk of black-tailed deer during lactation. J. Mammal. **58**, 421—423 • MUNRO, J. (1962): A study of the milk yield of three strains of Scottish Blackface ewes in two environments. Anim. Prod. **4**, 203—213.

PEART, J. N., J. M. DONEY and A. J. MACDONALD (1975): The influence of lamb genotype on the milk production of Blackface ewes. J. Agril. Sci. Camb. **84**, 313—316.

REITER, J., S. L. STINSON and B. J. LE BOEUF (1978): Northern elephant seal development: the transition from weaning to nutritional independence. Behav. Ecol. Sociobiol. **3**, 337—367 • ROBBINS, C. T., and A. N. MOEN (1975): Milk consumption and weight gain of white-tailed deer. J. Wildl. Mgmt. **39**, 355—360 • RUSSO, J. P. (1956): The desert bighorn sheep of Arizona. Ariz. Fish Game Dept. Bull. **1**.

SADLIER, R. M. F. S. (1969): The Ecology of Reproduction in Wild and Domestic Mammals. Methuen, London • SEKULIC, R. (1978): Seasonality of reproduction in the Sable Antelope. E. Afr. Wildl. J. **16**, 171—182 • SHACKLETON, D. M. (1973): Population quality and bighorn sheep (*Ovis canadensis*). Unpubl. Ph.D. diss. Univ. Calgary, Calgary • SIMMONS, N. M. (1969): The social organization, behavior, and environment of the desert bighorn sheep on the Cabeza Prieta Game Refuge, Arizona. Unpubl. Ph.D. diss., Univ. Arizona, Tucson • SPEDDING, C. R. W. (1965): Sheep Production and Grazing Management. Baillère, Tindall and Cox, London • STELFOX, J. G. (1974): Range ecology of Rocky Mountain bighorn sheep in Canadian National Parks. Can. Wildl. Serv. Publ. Ottawa, 234 pp.

THOMSON, W., and A. M. THOMSON (1953): Effect of diet on the milk yield of the ewe and growth of her lamb. Brit. J. Nutrit. **7**, 263—274 • TINBERGEN, N. (1965): Behavior and natural selection. Proc. Int. Cong. Zool. **6**, 521—542 • TING, I. P., and W. J. JENNINGS (1976): Deep Canyon: a Desert Wilderness for Science. Univ. Calif. Press, Riverside • TRIVERS, R. L. (1972): Parental investment and sexual selection. In: Sexual Selection and the Descent of Man, 1871—1971. (CAMPBELL, B., ed.) 136—179. Aldine-Atherton, Chicago • TRIVERS, R. L. (1974): Parent-offspring conflict. Am. Zool. **14**, 249—264 • TURNER, J. C. (1973): Water, energy, and electrolyte balance in the desert bighorn, *Ovis canadensis*. Unpubl. Pk.D. diss., Univ. California, Riverside • TYLER, S. T. (1972): The behaviour and social organization of the New Forest ponies. Anim. Behav. Monogr. **5**, 87—196.

WALLACE, L. R. (1948): The growth of lambs before and after birth in relation to the level of nutrition. J. Agril. Sci. Camb. **38**, 93—153 • WATKINS, W. E. (1943): Composition of range grasses and browse at varying stages of maturity. New Mexico Agril. Exp. Sta. Bull. **311** (cited from HEBERT 1973) • WELLES, R. E., and F. B. WELLES (1961): The bighorn of Death Valley. U.S. Nat. Parks, Fauna Ser. **6** • WILLIAMS, G. C. (1966): Adaptation and natural selection. Princeton Univ. Press, Princeton • WILSON, E. O. (1975): Sociobiology; the New Synthesis. Harvard Univ. Press, Cambridge.

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