

**PHYSICAL CONDITION AND SURVIVAL RATE  
OF CHAMOIS (*Rupicapra rupicapra* L.)  
AS A FUNCTION OF MATURITY-SEX CLASS  
RATIOS IN THE POPULATION:  
IMPLICATIONS FOR UNGULATE HARVEST PLANS**

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**CONDITION PHYSIQUE ET TAUX DE SURVIE  
DU CHAMOIS, *Rupicapra rupicapra* L.  
EN FONCTION DES CLASSES D'AGE ET DE SEXE  
DE LA POPULATION**

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In preparing an English version of this manuscript, I have added some clarifying footnotes (Stringham, 1980).

## ABSTRACT

Over a period of 4 years 1970-73, maturity-sex class ratios in a chamois population were experimentally altered, from a serious deficit of *mature* males to a nearly optimal balance of them with younger males and with females. Meanwhile, mean body, head, and heart weights of *prime* adult bucks increased 16%. Improvements among older bucks were almost as good. *Adolescent* bucks also showed consistent improvement. Weight changes among younger males and among females were not consistent from one variable to the next; nor were they statistically significant. This general pattern of improvement among *mature* and *adolescent* bucks, but lack of change among other classes of chamois, is thought to be a consequence of balancing maturity-sex infrastructure of the population -- via shortening of the rutting season and reduction of agonistic stress -- as well as of otherwise governing harvest so as to simulate and supplement natural selection pressures. Our strategy is thus called *Natural Selective Management*.

## INTRODUCTION

So long as gross over-harvest is avoided, it might appear as though trophy hunting has little detrimental effect on ungulate populations. But that is not necessarily true. At the 1971 *Ungulate Symposium* in Calgary, Anton Bubenik argued that typical hunter-harvests of ungulates, and virtual elimination of their major predators, have produced chronic, widespread deficits of prime adult males, which has in turn badly reduced the quality of ungulate populations in Europe, North America, and other parts of the globe. The project described in this paper was designed to test the hypothesized link between population health vs. adult male abundance. Data were collected on chamois (*Rupicapra r.*), red deer (*Cervus elaphus*), and roe deer (*Capreolus c.*). Preliminary findings on chamois are presented here.

Although various facets of Bubenik's hypothesis have been published for more than a decade in a variety of European languages, there is no detailed summary available in either German or English. Hence, Stringham undertook to do so by piecing together ideas taken from Bubenik's 1971 presentation at the *Ungulate Symposium*<sup>1</sup> and from conversations with him -- during which many of Stringham's own ideas became so interwoven with Bubenik's that it was no longer possible to separate which of us derived which ideas. Our approach to ungulate management might best be termed the *Natural Selective Management* hypothesis.

Hunting may partly compensate for lack of predation. But the number and quality of animals shot from each sex and age-class are not necessarily equivalent to what would have fallen prey. Age-sex infrastructure in heavily hunted populations tends to be quite different from those which are *naturally regulated*.<sup>2</sup> Under natural conditions, greatest mortality for ungulates tends to be among the very young and very old. Weak, sick, injured, and malformed individuals are quickly eliminated through frequent *testing* by predators. By contrast, for populations where predation has been minimized, culling rate can be markedly diminished -- or at least postponed -- in spite of the continued operation of other *natural regulators* such as pathogens, weather, and social strife. Poor quality individuals tend to survive longer, and more of them breed, potentially lowering average genetic and phenetic quality in the population. Pathogens have a greater chance of spreading. These deleterious effects of altering the natural mortality structure are accentuated by poor hunting practices that, in essence, reverse natural selection, by concentrating harvest on *mature* males in top condition, with plenty of meat and fat, and with trophy antlers or horns--the population's prime sires and social governors over adolescent males.

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<sup>1</sup> That paper, entitled *Social Wellbeing as a Special Aspect of Animal Sociology*, was not included in the proceedings of the Ungulate Symposium (Geist & Walther 1974).

Concentrating harvest on *mature* males can also substantially raise the level of social strife within a population. It is widely agreed among ethologists that a major function of rank hierarchy and territoriality is to maintain orderly, but fluid, agonistic interrelationships within an animal society, minimizing serious fighting and especially mortal combat. It is also recognized that removal of high-ranking or territorial individuals disrupts the *agonistic balance*, especially as it involves subordinates or non-territorials. Consequent intensification agonistic strife can be severe until the hierarchy or territorial system is readjusted. Furthermore, *adolescent* males tend to be much more energetic than *matures* in their agonistic activities, such as chasing and sparring.<sup>3</sup> Adolescents are more likely to fight where *matures* would merely threaten, for instance to re-establish or maintain relative rank. In a population where there are enough *matures* to dominate *adolescents* and dampen their aggression, social strife probably tends to be optimized. But when *mature* males are over-harvested, strife can become more dangerous to individuals, and more costly to the society.

Presumably, the older a male is, the more select he tends to be, and the greater his genetic value to the population as a sire. Thus, it is of advantage to avoid harvesting *mature* males until senescence is so far advanced that they don't breed or participate in the rank hierarchy or territorial system. We need sufficient young males to replace aging and dying *matures*. But an excessive proportion of *adolescent* males apparently decreases, rather than increases, the fitness of a population. Thus, the historical concentration by hunters on *mature* (high ranking or territorial) males has produced *chronic* social disorganization in ungulate populations throughout Europe and North America. The excessive energy costs, more frequent injuries, disruption of *adaptivity-generating social processes*, and other consequences have substantially increased mortality rate among adult males -- over and above what we shoot. These socio-pathological effects of chronic maturity-class imbalances can be seen year-around; but they are most profound during periods when males are establishing hierarchies or territories, or during the pre-rut or rutting seasons.

Other factors to consider are: (1) If the ratio of fertile females to potent males is so high that many does are not impregnated during their first estrus, or if they are so stressed that they abort, they may ovulate repeatedly until conception and implantation are successful. Engaging in rutting activities, not merely for a few weeks, but for months as females pass through successive estrus periods, might easily double the energy/nutrient costs of breeding for rutting males. Because rutting males tend to fast, this price is paid mostly from fat reserves. This excessive fat drain can lower probability of surviving the following winter, particularly if it is severe. (2) A *kid* conceived during a female's second or later estrus is born correspondingly later the next

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<sup>2</sup> When attempting to unravel the matrix of natural and artificial factors stressing an ungulate population, one must of course always consider what the mortality rate from a particular cause or matrix of causes would be under pristine conditions, before concluding that their *effects* are *natural*. The *coup de grace*, be it a predator or an avalanche, is only the last in a lifetime of stressors leading to the ungulate's death. Disturbance by people can drive chamois, for example, into areas where danger from avalanches is greater or food supply poorer than in preferred localities. Reduced nutrition in turn lowers resistance to such factors as cold, parasites, and predation. Also, the particular parasites infesting the ungulates may not be *natural* members of the ecosystem, but exotics introduced through livestock -- a situation that prevails on our own research area. Thus, phrases like death from *natural causes* or *natural regulation* need to be used with caution. In the strictest sense, *natural regulation* means regulation of not only total population size and density, or age-sex structure, but quality as well -- quality in the sense of the population's adaptive flexibility and ecological balance. (Stringham 1980).

<sup>3</sup> When *matures* do push one another past the point of ritualized sparring, and begin non-ritualized combat, this is typically more ferocious and lethal than fighting among *adolescents* (see also Walther 1965).

summer or autumn (in some cases as late as October), and may be too small and immature to survive the following winter. Or, if late-born *kids* do survive, they tend to be in poorer condition and more heavily infected with pathogens.

Together, these various consequences of sex- and maturity-class imbalances can severely reduce the survival potential of ungulates.<sup>4</sup> Geist (1971, pers. comm. to Stringham) reached similar conclusions for mountain sheep (*Ovis* spp.).

### Traditional Management Practices in Austria and Germany

Even by the end of World War II, game keepers in many parts of Europe had come to recognize the need for culling wild ungulates so as to reduce spread of pathogens and improve breeding stock, rather than indiscriminantly shooting the best trophy animals. But their efforts have at best been only a rough approximation of natural selection pressures. For one thing, culling was aimed primarily at production of trophies. The individuals with poorest horns or antlers were removed, with little regard for whether the deficiencies were genetically vs. epigenetically (environmentally) determined, or for long-term quality of the populations. Breeding domestic animals to accentuate certain characteristics has often produced types unfit for survival in the wild. So too, culling primarily to increase horn or antler quality -- according to arbitrary, not biological standards -- may in the long-run be detrimental to the animals. While selection to preserve the healthiest, best-adapted individuals would tend to produce good trophies, the reverse is not necessarily true. Culling for trophies may be better than no culling, but it isn't adequate.

## PROCEDURES

### Harvesting to Simulate and Supplement Natural Selection

Prior to initiation of our project, management practices on the study site, Achenal-West, followed traditional emphasis on trophy production. However, since 1970, the choice of which chamois to shoot has been based as much as possible on biological considerations. Only after all (of what the game keepers can recognize as) physically poor specimens have been shot, is our harvest focused on those with inferior horns. No special effort is made to remove chamois whose horn deformities are due to injury, since the deformities will not be passed to their offspring. Nor do the horn deformities appear to be a serious social or ecological handicap. The best trophy bucks and does are normally shot only when they are too old to breed or to perform other social functions, or when their condition begins to deteriorate.

Bubenik's harvest plan is also designed to maintain biologically sound maturity-sex or age-sex class ratios in each population. As detailed in Bubenik & Schwab (1975), Bubenik distinguishes five stages of sexual ontogeny in chamois: *kids*, *pre-adolescents*, *adolescents*, *primes*, and *seniors*. *Kids* are chamois up to about 1 year old, nearly all of whom accompany the mother. *Pre-adolescents* have, in general, become independent of their mothers; but they have not yet completed puberty. In our population, nearly all yearlings and most 2-year-old bucks fall into this category. *Adolescents* have completed puberty, but are not fully mature sexually -- in terms of either appearance, physiology, or behavior. They are highly aggressive, in much the

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<sup>4</sup> Although Bubenik sometimes refers to specific species, he often just uses the term *ungulates* without indicating which species this has been documented for, or whether any exceptions are known. So suffice it here that these ideas are thought applicable to chamois, red deer, and roe deer, as well as apparently to mountain sheep. Note, however, that roe deer delay implantation, and thus may show less spread in fawning dates as a consequence of lengthening the rut.

ame way as human teenagers, and markedly less inclined than *matures* to conduct agonistic encounters ritualistically. *Primes* are *mature* males and females in optimum reproductive condition. *Seniors* are post-*prime*, and eventually cease to reproduce and to participate in contests for rank or territory. Although Bubenik has estimated that senescence begins with age 10 for bucks, they probably continue breeding at least through age 13. The transition from *prime* to *senior* is gradual. A comprehensive discussion of criteria distinguishing each maturity-class will be presented in Bubenik's forthcoming book on nutrition and social well-being in ungulates. Let it suffice for now to mention that the terms *adolescent* vs. *mature* correspond fairly closely with some uses of *adolescent* or *subadult* vs. *adult*, respectively. But, because of the ambiguity of those latter terms, their use is avoided here. Although each maturity-class is characterized by a special range of ages, the reader is cautioned to keep in mind that the maturity vs. age relationships at Achensee-Northwest may differ from those in other populations; in some maturation may be faster, and in others slower.

Because there are no adequate data available on sex- and maturity-class ratios in pristine populations of chamois, the optimum ratios were estimated by Bubenik, based on information in the literature and upon his own observations of chamois in heavily hunted, infrastructurally-disrupted populations, and of red deer, roe deer, and other ungulates, in both naturally regulated and heavily hunted populations. As culling proceeds and its effects are noted, and as data from our concurrent investigations of physiological parameters become available, our notions of what ratios are optimum will be refined accordingly. Our current estimates are given above in Table 1. These target values are thought of as approximations of the *median* of each allegedly optimal range. By striving to achieve these target values each year, we expected to maximize the probability of maintaining each ratio within its optimal range, despite the unavoidable imperfections of censusing and in selective harvesting, and despite unpredictable effects of weather and other factors. Optimal sex ratio was estimated as 85-100M:100F when all maturity-classes were considered together, and as about 75-85M:100F among *matures*.

### Study Area and Geographic Barriers to Migration

The study area, Achental-West (abbreviated Achental-W) lies within the Karwendel Range of the Tirolean Alps, about 30 km northeast of Innsbruck, Austria. To the south and southwest lie the adjacent estates of Seekarspitz, Seeberg, and Gern; Bächental-East (Abbreviated Bächental-E) adjoins Achental-W to the west, and Hünnerberg-Dürnberg borders it to the northwest. Together, the 6 estates constitute the geographically isolated habitat herein called Achensee-Northwest (Achensee-NW) (Fig. 1). It can best be visualized as a peninsular arm of a mountain, *separated* from rest of the mountain to the south by steep slopes and cliffs; to the west, north, and east, Achensee-NW is bounded by a continuous chain of gorges, valleys, bodies of water, highways, and villages. These natural and artificial barriers minimize migration by chamois into or out of Achensee-NW, according to our game keepers. (The keepers are professionals who spend nearly every day of the year in the field with these animals and keep close track of where a large proportion of the chamois can be found). These barriers are not so much impassable as avoided. Chamois can negotiate even cliffs and might be able to swim across the lakes; they could sneak through towns and villages at night. But there is no indication that they do so. They seem to prefer steep slopes (Schröder, pers. comm.) and seldom venture onto or across the broad flat valleys -- valleys that are frequented and traversed by red deer and some roe. Chamois likewise seldom cross the steep rocky slopes which form the southwestern boundary of Achensee-NW, because the slopes are nearly bare of food. So, although the population of chamois within Achensee-NW may not be isolated enough to be considered a *deme*, we have no basis for thinking that migration into or out of the area is substantial enough to bias the phenomena we are investigating.



**Table 1.** Approximate median values for the target ranges of maturity-class ratios in chamois.

Males			Females		
Class & Age	% of all males	% of all males $\geq 1$ yr	Class & Age	% of all males	% of all males $\geq 1$ yr
Kid <1yr	18		Kid <1yr	15	
Pre-adolescent 1-2yrs	23	28	Pre-adolescent 1 yr	11	13
Adolescent 3-4yrs	16	20	Adolescent 2-3yrs	16	19
Prime 5-9yrs	33	40	Prime 4-11yrs	46	54
Senior $\geq 10$ yrs	10	12	Senior $\geq 12$ yrs	12	14

By contrast, there are no major topographic barriers to travel within Achensee-NW; all chamois there are members of a single population, regardless of which estate they reside in during any given part of the year. To avoid ambiguous usage of the term *population*, residents within each estate will be described as a *residation*.<sup>5</sup> For example, the Achental West *residation* consists of all chamois having activity centers there during a given season. Membership of each *residation* changes somewhat within each season as individuals move from place to place; but the major shifts are seasonal, as described below. This distinction between *population* vs. *residation* is crucial for interpreting our data, particularly in terms of how the new pattern of harvest -- begun in 1970 at Achental-W and in 1972 at Bächental-E and Seekarspitz -- affected the population as a whole. First, these are the only *residations* where we could control the pattern of harvest; traditional methods continued in the other three estates. Second, that is where nearly all of our data came from. In other words, we have data on year-to-year changes in quality and age-sex structure of the Achental-W, Bächental-E, and Seekarspitz *residations* -- changes that were associated with and presumably produced by our manipulations. But these *residations* constitute only about half of the Achensee-NW population, the other members of which also have to be taken into account.

### Distribution of Chamois Within Achensee NW

Although many chamois regularly moved back and forth across the ridgeline dividing Achental-W from Bächental-E, there was much less movement across borders lying perpendicular to the ridgeline. So while a fraction of the chamois censused in Achental-W or Bächental-E cannot realistically be thought of as residing in one estate or the other, most can be distinguished as residing in that combined area vs. outside of it.

### Activity Centers During Late Spring and Summer

*Mature* and *adolescent* does and *preadolescents* of both sexes living above timberline moved freely back and forth across the ridgelines as they fed. This occurred even in the absence of *obvious* motivating factors. But such movements were especially common in response to weather. For instance, chamois might seek the lee side during high winds. On a hot day, when they sought shade, the morning would be spent on the west slope, the afternoon on the east slope. The reverse pattern was seen on cold days. *Mature* and *adolescent* bucks restricted their activities more to specific locations and could reliably be found there day after day by the game keepers.<sup>6</sup> Although bucks living above timberline also crossed the ridge in response to weather, they seemed to require more provocation than did does and young. By contrast, chamois living below timberline--the so-called *woods chamois* -- seldom moved over the ridge except in the most extreme weather, although they crossed seasonally, with the onset of autumn or winter.

### Activity Centers During the Remainder of the Year

According to our game keepers, the bucks became more mobile in early or mid-autumn. In fact, chamois of all classes with summer activity-centers in Achental-W moved over the ridge to Bächental-E, remaining there throughout the rutting season and winter. Bächental-E may attract Achental-W bucks during rut because the density of rivals in Bächental is lower than in

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<sup>5</sup> In the manuscript serving as the basis for translation into French, the term *geographic-population* was used to distinguish this concept from a *social-population*. However, some readers have difficulty keeping in mind the distinction between *g*- vs. *s*-populations. So the term *g*-population was replaced here by *residation* -- residents at a given time. (Stringham, 1980).



Achental-W -- as will be discussed later. Furthermore, all classes favor the Bächental slope over the Achental slope during winter, presumably because Bächental-E receives more sun and is kept freer of snow by avalanches and by wind.

Censuses were conducted during summer and most accurately reflect age-sex structures and relative sizes of the different *residations* during that season. But they are not representative for rest of the year. At best, bias can be minimized by considering the Achental-W and Bächental-E *residations* together, since most membership exchange is between them. Granted, there is some seasonal *migration* of chamois across the border separating those 2 estates from Seekarspitz to the south and across Hünnerback gorge to the northwest (see Fig. 1). In fact, it would be most reliable to evaluate impacts of our hunting policy on the Achensee-NW *residation* as a whole; but adequate data are simply unavailable, as will be explained below. In fact, for various reasons this manuscript had to be limited to consideration of changes in the Achental-W *residation* relative to our hunting policy. Our next paper will encompass changes in the Bächental summer *residation*.

### Size and Composition of the Achental-W *residation*

#### 1974 Census

The only reliable census of the Achental-W summer *residation* was made one morning in July 1974. Several experienced game keepers climbed from the lower flank of the mountain arm (Achensee-NW) upward past timberline to the crest which separates Achental-W from Bächental-E. As they climbed, all chamois seen were counted; age and sex were estimated. A simultaneous count was made on the Bächental-E slope. Precautions were taken to minimize duplicate counting of chamois that crossed the ridge, and thus might be seen on both slopes during the census. The fact that some individually known bucks and does were not seen during the census led our chief game keeper to estimate that the census encompassed about 90% of all chamois living above timberline, but only a small fraction of those living below timberline--roughly one-third of the total *residation*. However, since individual *woods chamois* could usually be found at predictable activity centers, their numbers and age-sex class structure were estimated from observations over several weeks before and after the principal census day. When all of this information was pooled, it yielded the maturity-sex class ratios shown in Table 2.

Under the circumstances of censusing, evaluation of sex and age of each chamois was based on appearance, particularly horn morphology. Sexual dimorphism is apparent by age 2 years. Age polymorphism, by contrast, diminishes with maturity. In the field, horn structure is a reliable age cue for a professional game keeper, with a precision of about  $\pm 1$  year up to age 4, and at best  $\pm 2$  years thereafter. (Granted, annual horn-rings can enable one to count age of animals even 12 to 15 years old; but rings are seldom visible under field conditions.)

#### Estimated Infrastructure for 1970-73

Lacking reliable field counts of chamois prior to 1974, census figures for earlier years can only be estimated. One method is population reconstruction. For instance, suppose that:

- 1) In July 1974 we had been able to accurately census all of Achental-W and had counted 30 seven-year-old bucks.
- 2) We had shot 5 six-year-old bucks during the 1973 season, and had found 2 more dead from avalanches that winter. We could conclude that *at least* 27 six-year-old bucks lived there during July 1973.

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Bucks in this area of Austria maintained small activity centers during summers. Agonistic activity seen may have been spatially defensive. So these areas were called *territories* even though Kramer (1969, pers. comm.) observed territorial formation and defense only during the autumn rut among chamois in Switzerland. (Stringham, 1980).

**Table 2. Maturity-class infrastructure of Achenal-West chamois:**  
 absolute numbers and proportions of individuals in each class  
 (excluding kids) during summers 1970-74.

Class & Age	Target	Estimated number and proportion (%) of chamois of each sex that are >1 year old				
		1970	1971	1972	1973	1974
<b>MALES</b>						
Kids (<1 yr)		25	47	21	33	28 <sup>a</sup>
Pre- adolescent 1-2 yrs	(28)	55 (36)	35 (22)	54 (33)	40 (25)	33 (20)
Adolescent 3-4 yrs	(20)	61 (40)	75 (48)	38 (23)	30 (19)	35 (22)
Prime 5-9 yrs	(40)	33 (22)	45 (29)	72 (43)	88 (54)	87 (54)
Senior ≥10 yrs	(12)	3 (2)	1 (1)	2 (1)	4 (2)	7 (4)
TOTAL						
All		177	203	197	195	190
No Kids		152	156	166	162	162
<b>FEMALES</b>						
Kid (<1 yr)		26	36	26	36	28
Pre- adolescent 1 yr	(13)	19 (12)	24 (15)	26 (17)	15 (11)	25 (19)
Adolescent 2-3 yrs	(19)	63 (40)	53 (32)	40 (27)	44 (32)	25 (19)
Prime 4-11 yrs	(54)	71 (46)	81 (50)	78 (53)	78 (57)	78 (58)
Senior ≥12 yrs	(14)	3 (2)	5 (3)	4 (3)	0 (0)	6 (4)
TOTAL						
All		182	199	174	173	159
No Kids		156	163	148	137	134

This assumes, of course, negligible net migration into or out of Achental-W from year-to-year. As a first approximation, the risk entailed by this assumption seems warranted. In a subsequent paper, data for both Achental-W and Bächental-E will be pooled. There is definitely negligible annual migration in/out of that larger area.

There are 3 reasons why this preliminary paper focuses on changes in the structure of the Achental-W *residation*:

- 1) That is where our new hunting scheme was first introduced.
- 2) Sex- and age-specific data on mortality and body condition of all animals shot has been gathered in Achental-W since 1970; specific mortality data were not collected in Bächental until 1972, and the other types of data weren't collected there.
- 3) Space limitations herein don't allow presentation of population structure data on both estates, separately as well as jointly.

### Statistical Analysis

When comparing body, head, organ and fat weights between the two periods 1970+71 vs. 1972+74, significance of differences was evaluated using the 1-tailed t-test, as modified for finite populations (Freund 1967:209-210, 234). Regression lines and correlations were done by Pearson Product Moment Least Squares Analysis (Freund 1967).

## RESULTS

### Maturity/Age and Sex Infrastructure

Table 2 shows the maturity-class infrastructure of Achental-W chamois from 1970-74, for both bucks and does. Note that it presents absolute numbers of chamois counted in each class, as well as the percent of the total *residation*, excluding *kids*, constituted by the class. *Kids* are omitted in this latter calculation because the number counted isn't representative of the population. The maturity-sex class ratio figures are based on our 1974 census, and on reconstructed values for 1970-73, derived from records of harvest and *natural* deaths.

The proportion of *mature* does increased about 30% from 1970-74. Average doe age (excluding *kids*) increased from 4.4 years to 4.8 years. This trend was even stronger among bucks. The proportion of *pre-adolescent* and *adolescent* males was roughly halved during this period, while that of *mature* bucks was doubled -- an increase in average age from 3.6 to 5.2 years. It will be noted that while there are still too few *senior* bucks, this deficit will eventually be filled from the current temporary excess of *prime* bucks as they mature.

Prior to 1970, we have no data on sex ratios or the maturity-class infrastructure of our Achental-W residents. Harvest there had traditionally been concentrated on trophy males and old females even more exclusively than was the case in Bächental. The *census* figures for Bächental from 1955-69 (which counted no more than 50% of the chamois present) indicate that the sex ratio excluding *kids* averaged 73M:100F (range 64-80M:100F). The ratio in Achental-W may have been even lower.

Following the severe winter of 1969, which decimated chamois populations throughout the Karwendal Range, the sex ratio (excluding *kids*) in Achental-W was 97M:100F; but there was a strong deficit of *mature* bucks, relative to young males (Table 3). This deficit continued through summer 1971. By 1972, the target sex ratio for *matures* had been achieved during the *summer*. During the summers of 1973 and 1974, there seems to have been a surplus of *mature* bucks in Achental-W. By contrast, comparable census data for Bächental-E indicate a deficit of *mature* bucks even as late as 1974 (46M:100F). However, it is doubtful that this large local difference in proportions of *mature* bucks was maintained during the rut. We know that some bucks with

**Table 3. Sex ratios in Achenal West during Summers 1970-74.**

Maturity Classes	Numbers of M/100F					
	Target	1970	1971	1972	1973	1974
Total population	85-100	97	102	107	113	120
Total w/o Kids	82- 96	97	96	112	118	121
Adolescents + Primes + Breeding Seniors	76- 89	72	89	94	100	123
Primes + Breeding Seniors	73- 86	59	55	94	118	118

**Table 4. Winter-mortality 1969/70 - 1972/73 in Dollmannsbach,  
Pitz, Bachental, Seekarspitz, Hechenberg, and Klammbach.**

Classes	Winter				Total
	1969/70	1970/71	1971/72	1972/73	
Kids	61	5	5	25	96
Does	38	11	5	20	74
Bucks	51	5	15	19	90
TOTAL					
All	159	21	25	64	
No Kids	89	16	20	39	

summer activity centers in Achental-W and some of our does move to Bächental-E in autumn, as discussed earlier. Such seasonal shifts in activity centers appear to distribute males and females in a much more equal ratio over the combined area in autumn and winter than is the case during summer. Thus, it is of interest to note that when average sex ratio is calculated for the 2 estates together, the proportion of *mature* bucks to fertile *mature* does has been within the target range since 1972. Furthermore, maturity-class ratios, especially for bucks, in the combined areas were progressively better in 1972 and 1974.

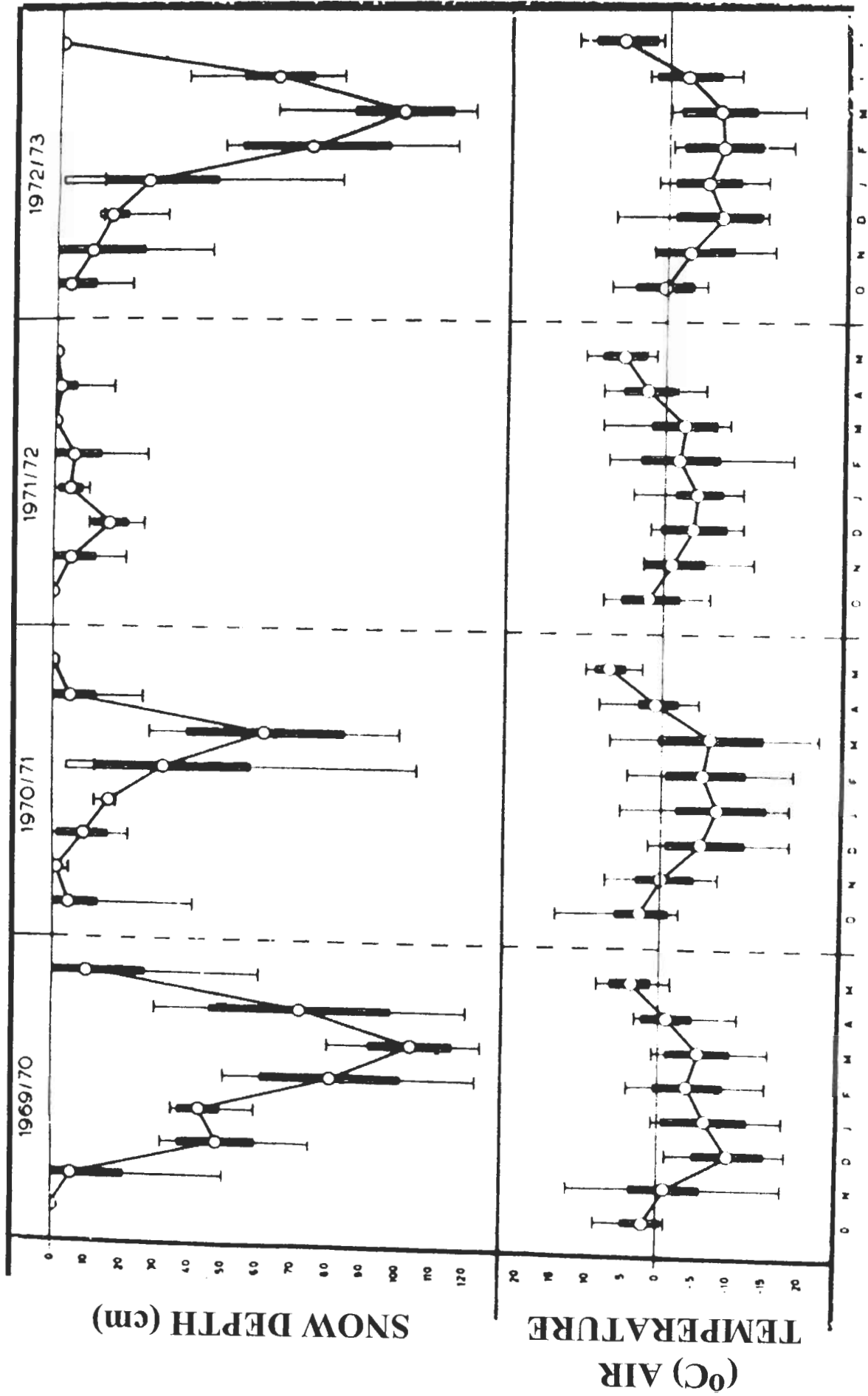
Census data for the other estates in the Austrian sector of Achensee-NW is less reliable, but nevertheless worth considering. We seem to have had an adequate sex ratio among *matures* since 1972 (the first year for which we have class-specific data); in fact, figures suggest a surplus of *mature* bucks in 1974 (99M:100F). Census data for Hünnerberg-Dürnberg in Germany are also very limited. An estimated 40% of the *residation* died during winter 1969/70; *residation* size then increased from about 45 chamois in 1970 to 61 in 1975. There too, sex ratio (excluding *kids* and yearlings) has been about 1:1.

### Population Density

*Referring back to Table 2:* Calculations indicate that in Achental-W, the total number of bucks, excluding *kids*, has varied little since 1970, although the number of does may have declined--due to our increased hunting pressure on females. Total number of bucks + does in Achental-W has remained very constant. When we combine data from Achental-W with information from Bächental-E, we find that numbers of both sexes have remained nearly constant since 1971 for the combined area. Nor is there any indication that density of chamois in the Austrian sector of Achensee-NW has changed much during the past few years (941 in 1972, 906 in 1974, a 4% decline). Although density appears to have remained fairly constant in Achental-W (7/100 ha) between 1970-74, that period may have been preceded by a fairly large die-off during the severe 1969/70 winter. We have no data on natural mortality in Achental-W during that winter; but we do know that at least 25% of the chamois in Bächental (East + West) died: carcasses of 42 *kids*, 24 does, and 42 bucks were found the following spring. The density of chamois in Bächental-W was at least half-again as high as in Bächental-E and on our estate, and the climate (snow depth and air temperature) in Bächental tends to be harsher than in Achental. So it is unlikely that such a large proportion of our the Achental-W *residation* was killed that winter. These considerations suggest that population density prior to winter 1969/70 would not have been higher than 10/100 ha; when data for Achental-W are lumped with data from Bächental-E, the net density-index was 8/100 ha since 1972. Therefore, taking into account the incompleteness of the censuses, the actual 1970-74 density for the 2 estates combined may have been as high as 9/100 ha, compared to 12/100 ha in summer 1969.

### Meteorological Influences

Thus far, the only weather data available to us are the air temperature and snow depth measurements made on the floor of Achental valley (by O. Obrist, of the Tiroler Wasserkraftwerk station, Seeache). The values of both variables assuredly differ from those a few hundred meters higher in elevation where the chamois live. But the Seeche values at least provide an indication of *relative* variation from month-to-month and year-to-year (Figs. 2 and 3). This is substantiated by the correspondence between the measures for snow depth each year versus the number of dead chamois found the following spring in Achental-W (Table 4; these data were collected only in Subunits Pitz, Dollmannsbach, Hechenberg, and Klammbach) and the adjoining estates of Seekarspitz and Bächental.



MONTH (Oct. - May)

Fig. 2. Air temperature and snow depth (mean, range, and 95% CB). Measures made each evening at 7pm at the Tyrolian Hydroelectric Station meteorological station in Seeach, Anchtental.

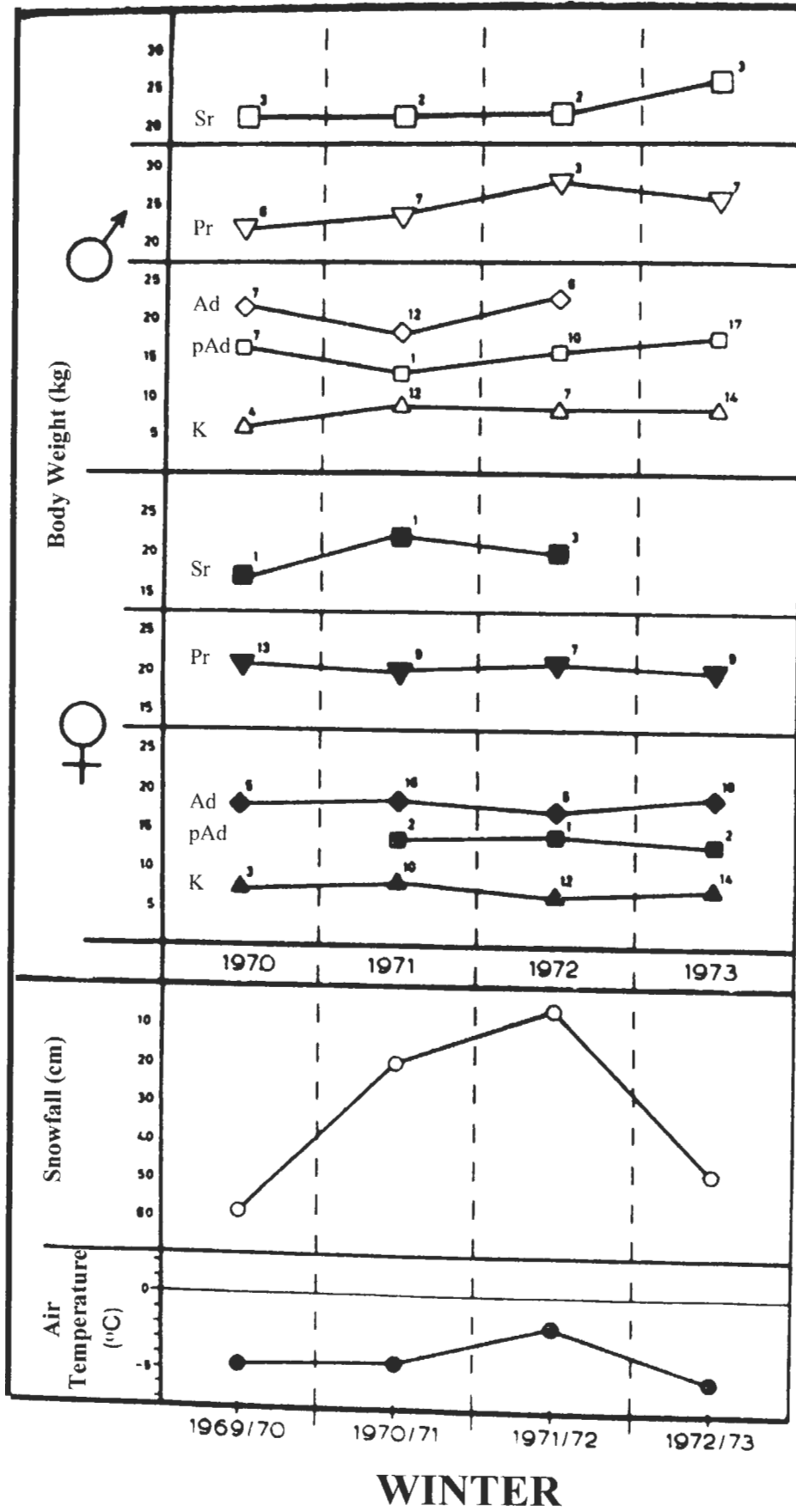


Fig. 3. Correlations between body weight and winter weather - annual means.  
 K = kids, pAd = preadolescent, Ad = adolescent, Pr = prime adult, Sr = Senior.

### Weight Changes in Harvested Chamois

To begin with, the reader should note that calculated changes in *mean* weights for *kids* are biologically *meaningless*; weight gain is so rapid during the first months postpartum, one can reliably compare only *kids* of known age; but we have no method of distinguishing age that is precise enough. It is seldom possible to distinguish whether an unusually immature *kid* (for the month in question) was merely born later than normal or developmentally retarded. This problem is accentuated by the fact that birth dates can range over a period of months. Although late-born *kids* constitute only a small proportion of the total, it is on them that our *kid* harvest is focused after all sick, malformed or injured ones have been shot. This is done to eliminate lactational stress on these dams and facilitate their recovery to high nutrient-energy balance -- enabling them to produce a better quality *kid* the following year. This culling appears to increase reproductive success of the females and productivity of the herd.

In the original manuscript presented in the Symposium, our graphs were based only on the actual data measured. All data available on each parameter (body weight, head weight, and so on) were included. However, that tends to be somewhat misleading. Since organs are commonly mutilated when an animal is shot, we have data on all organs for only a few individuals. The plot for heart weight vs. age, for example, was not strictly comparable to that on head weight, for each data set included and excluded some individuals that the other set did not. Therefore, rather than confine current comparisons to that small fraction of individuals for whom we have data on all parameters, weight values of mutilated organs (and of the few bodies that were not weighed) were estimated from weights of the individual's intact organs or from body or head weight, based on linear regression calculations between all pairs of parameters. Interpolations were made only where the correlation coefficient was at least 0.85 (Table 5). All correlations are significant ( $P < 0.01$ ). Any error thus introduced is too small to significantly bias our analysis of weight changes in response to changes in population infrastructure.

Although Bubenik estimated senescence as beginning in the 10th year of life for a chamois buck, only one of the *senior* bucks shot was over 13 years old, and only his testicular activity was subnormal. Thus, all but that 1 buck were probably as active in rutting activities as *primes*, and played essentially the same social roles. It is for this reason that data for *primes* and *seniors* are evaluated both separately and combined, as *matures*. Standard error of the mean is in all cases smaller for *matures* as a group than for either *primes* or *seniors* separately -- substantiating the interpretation that our *primes* and *seniors* are functionally equivalent in the social life of the herd. By contrast, *adolescents* play different social roles than *matures* during the rut; so one would not be justified in lumping data on *adolescents* with data on *matures*.

### Hog-Dressed Body Weight

Fig. 2 shows monthly changes in air temperature and snow depth. In Fig. 3, the mean values for each winter (Nov.-April) are shown, so that they can be compared with winter-kill information and body weight data. Values for body weight are from the hunting season (Aug.- Dec.) that *followed* each winter. In general, there is no obvious relationship between air temperature or snow depth during a given winter vs. body weights of chamois harvested during the following autumn. Granted, there is a superficial similarity between weather trends versus body weight of *prime* males; but we cannot regard this parallel as meaningful in lieu of additional information as to why *prime* bucks would be more affected by weather than are the other age-sex classes. This is not to suggest that body weight is not affected by severity of the preceding winter. But it is to point out that the only weather information available to us is not obviously a good indicator of such relationships.



**Table 5. Linear relationships between weights of body parts.**

Sex	X	Y	r	n	SE	Regression Equation
MALE	Body	Head	0.85	118	202	$Y = (4.54 \times 10^{-2})X + 331$
	Head	Body			3369	$Y = (16.1)X - 731$
	Body	Heart	0.73	106	51	$Y = (7.18 \times 10^{-3})X + 72.3$
	Head	Heart	0.88	97	35	$Y = (1.71 \times 10^{-1})X - 0.549$
	Heart	Head			180	$Y = (4.57)X + 248$
FEMALE	Kidney Fat	Kidney + Belly Fat	0.95	87	230	$Y = ((3.14)X + 28.4$
	Belly Fat	Kidney + Belly Fat	0.99	87	97	$Y = (1.38)X + 25.8$
	Body	Head	0.92	112	127	$Y = (4.98 \times 10^{-2})X + 252$
	Head	Body			2356	$Y = (17.1)X - 2026$
	Body	Heart	0.86	102	28	$Y = (7.72 \times 10^{-3})X + 43.9$
	Head	Heart	0.88	102	27	$Y = (1.47 \times 10^{-1})X + 12.39$
Heart	Head	161			$Y = (5.22)X + 174$	
Kidney Fat	Kidney + Belly Fat	0.96	82	144	$Y = (3.47)X + 30.3$	
Belly Fat	Kidney + Belly Fat	0.99	82	64	$Y = (1.35)X + 13.2$	

A *hog-dressed* animal has been eviscerated but has its head and hide intact. As will be noted in Fig. 4, body weight increased for all classes of males from 1970+71 to 1972+73. *Kids* increased 5%, *pre-adolescents* 7%, and older classes at least 15%. For *adolescents*  $P=0.10$ , *primes*  $P=0.01$ , *seniors*  $P<0.01$ , and total *matures* ( $P<0.005$ ). Among females, the only significant change was among *kids*; and that is not biologically meaningful, as explained earlier.

### Head Weight

Heads were weighed with hide, horns, etc. intact. Head weights (Fig. 5) showed virtually the same trends as body weight. We found no significant change among females in any class. Nor did heads of male *kids*, *pre-adolescents*, or *adolescents* increase significantly ( $P>0.10$ ). Head weight for *matures* increased 13% ( $P<0.001$ ). The greatest increase occurred among *primes* ( $P<0.01$ ), that class of adults which includes individuals that were *adolescents*, and thus still growing, in 1970 when we began balancing the sex- and maturity-class ratios of the Achenal-W residation.

### Heart Weight

Hearts were weighed with fat and other tissues intact. Heart weights did not change significantly (Fig. 6) among females or among *kid* and *pre-adolescent* males. The increases of 9% ( $P<0.15$ ) for *adolescents* and 10% ( $P<0.10$ ) for *senior* bucks are at best marginally significant. The 16% increase in heart weight for *prime* bucks is significant ( $P<0.02$ ), as is the 14% ( $P<0.01$ ) increase for *matures* (*primes* + *seniors*).

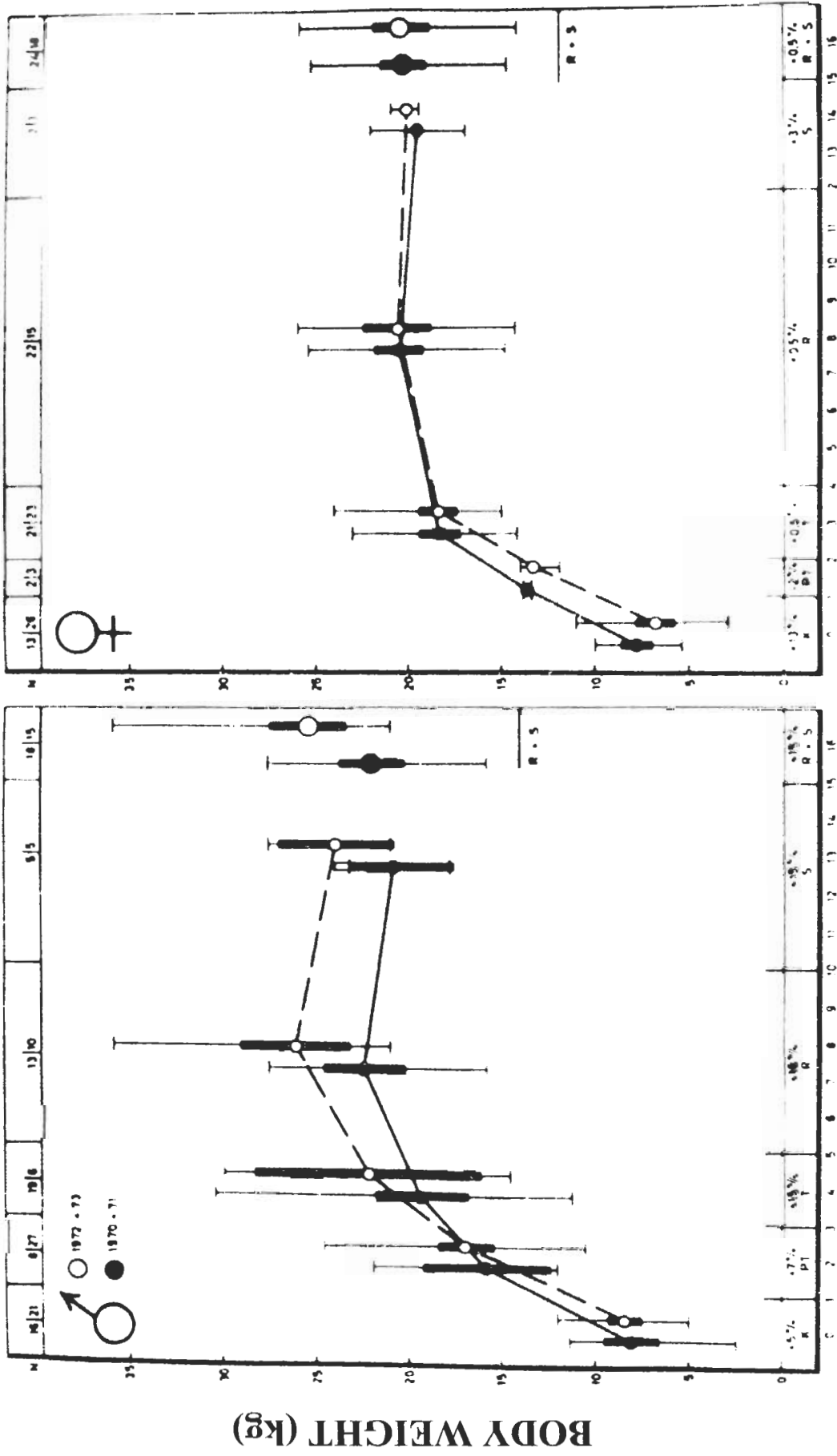
Unfortunately, we were not able to gather data on how much of these changes in weights of body and head were due to changes in subcutaneous or intramuscular fat deposits, rather than to changes in muscle mass, etc. Nor do we have information on how much the change in heart weight involved increase in epicardial fat rather than muscle, etc.

### Visceral Fat Weights

Visceral fat occurs primarily around the kidneys or attached to mesenteries. This was termed *kidney fat* and *belly fat*, respectively. There was seldom any problem distinguishing these fat deposits from one another.

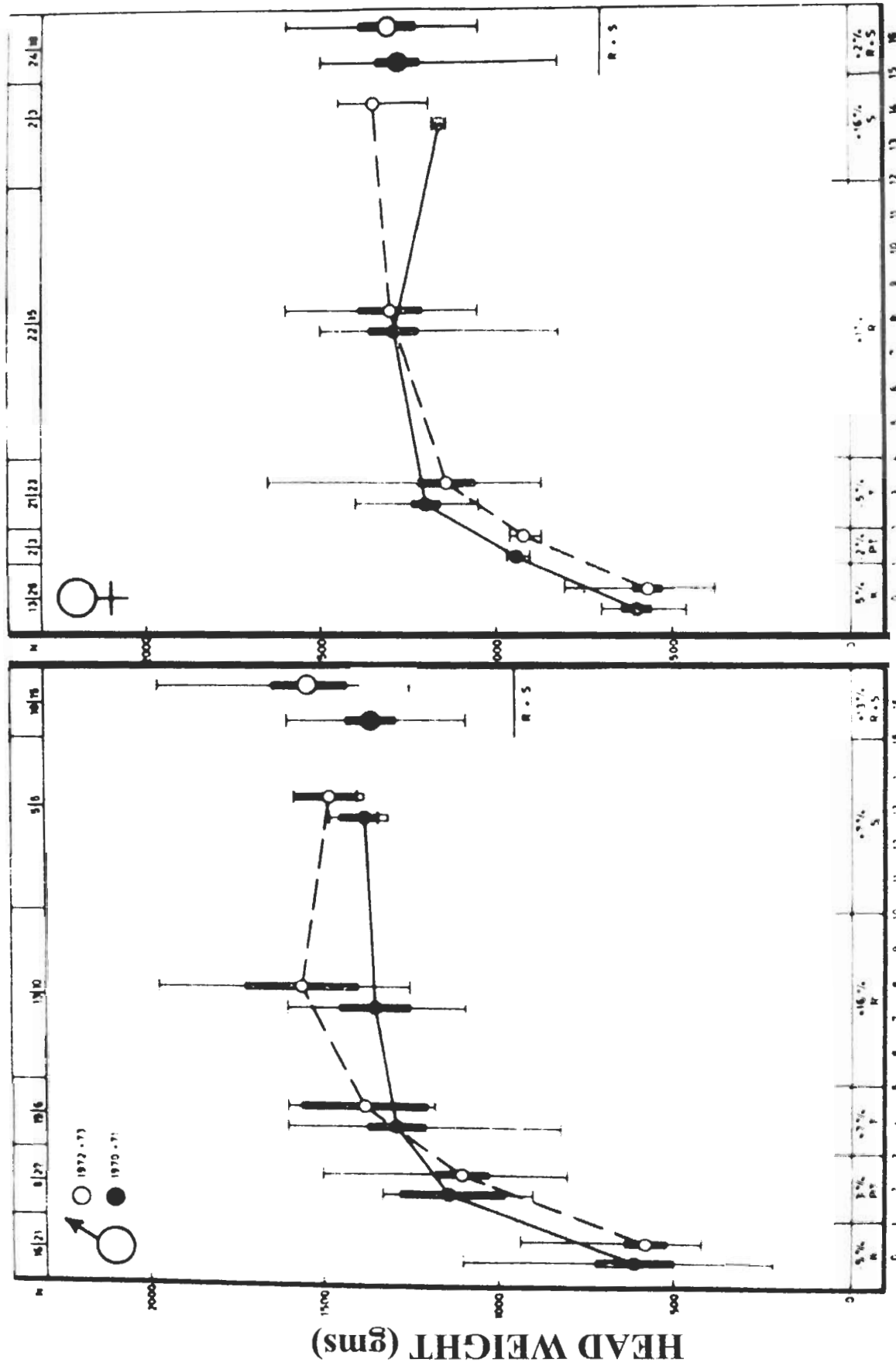
Especially for females, the pattern of changes in fat weight (Fig. 7) are different from those for the body, head, or heart. We found marked changes among *adolescent* and *prime* bucks, as well as among some classes of female. The only significant changes were for *adolescent* females ( $P<0.005$ ), *prime* bucks ( $P<0.05$ ), *adolescent* bucks ( $P<0.10$ ), and *seniors* ( $P<0.10$ ) of both sexes.

Biological interpretation of these results must proceed cautiously, due to the great changes in fat weight from month-to-month for a chamois. These graphs encompass data from August-December--a period over which harvest was *not* uniform. The numbers of individuals shot from each class and sex varied from month to month. Thus, to reliably compare fat data for 1970+71 with that for 1972+73, it would be necessary to first analyze seasonal changes in fat deposits. It would be desirable to standardize all data for a certain date, at the end of the rut for instance. That is, fat weight that the animal had or would have had at a standard point in time could be estimated from fat weight on the day it was shot. Then comparisons between years could be made with, hopefully, much less likelihood of bias. It would be revealing to compare the seasonal curves. Are peak and minimum weights higher in 1972+73 than in 1970+71? Did weight decline more gradually during the latter 2 years than during the former? At what weeks or months are peak and minimum weights reached? Answers to these questions would help reveal how balancing social structure influences energy intake and expenditure. Eventually, we



### AGE (years) & CLASS

Fig. 4. Body weight relative to age ● 1970+1971 vs. ○ 1972+1973. Values shown are mean, range, and 95% CB.



### AGE (years) & CLASS

Fig. 5. Head weight relative to age ● 1970+1971 vs. ○ 1972+1973.

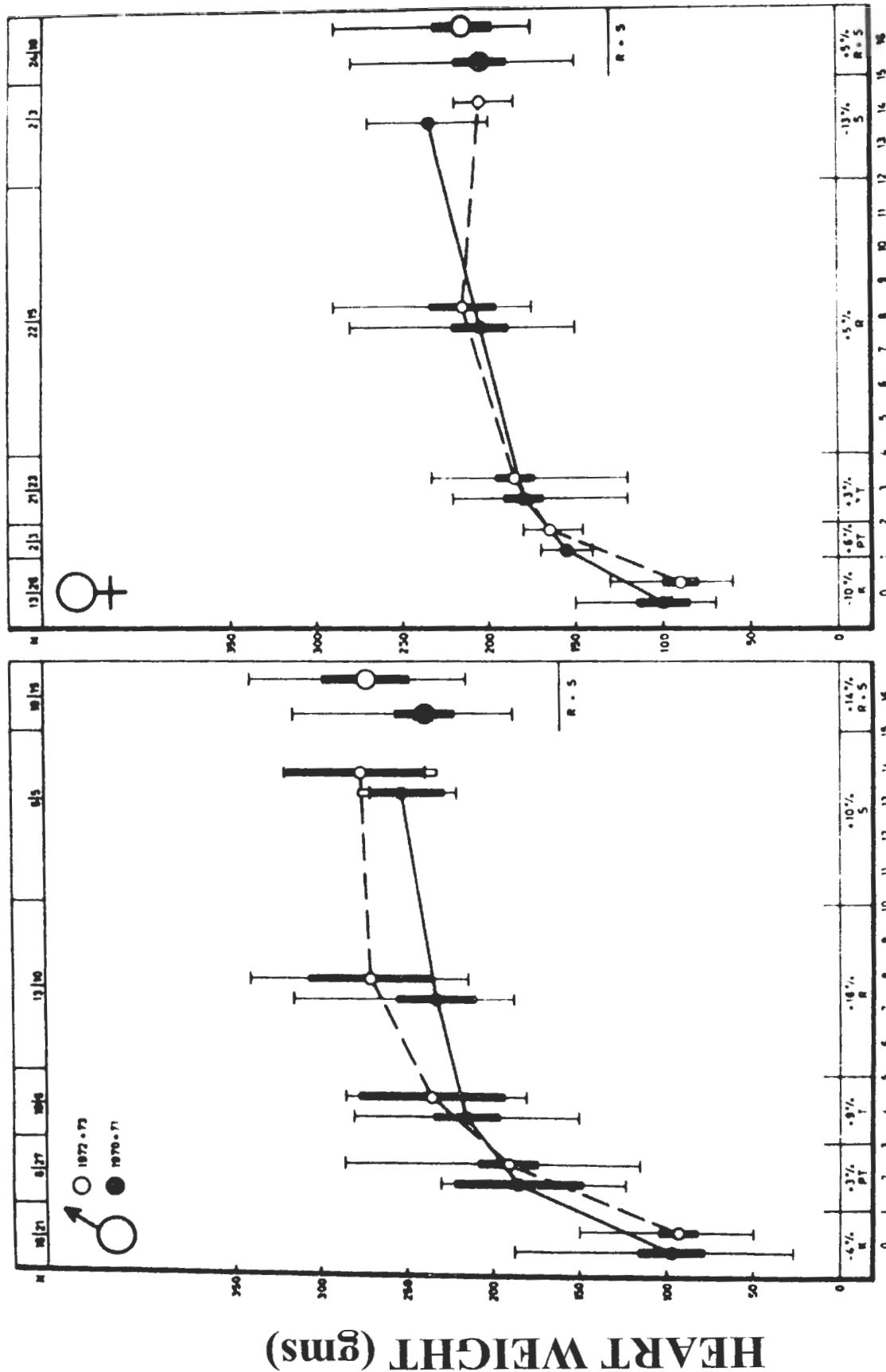
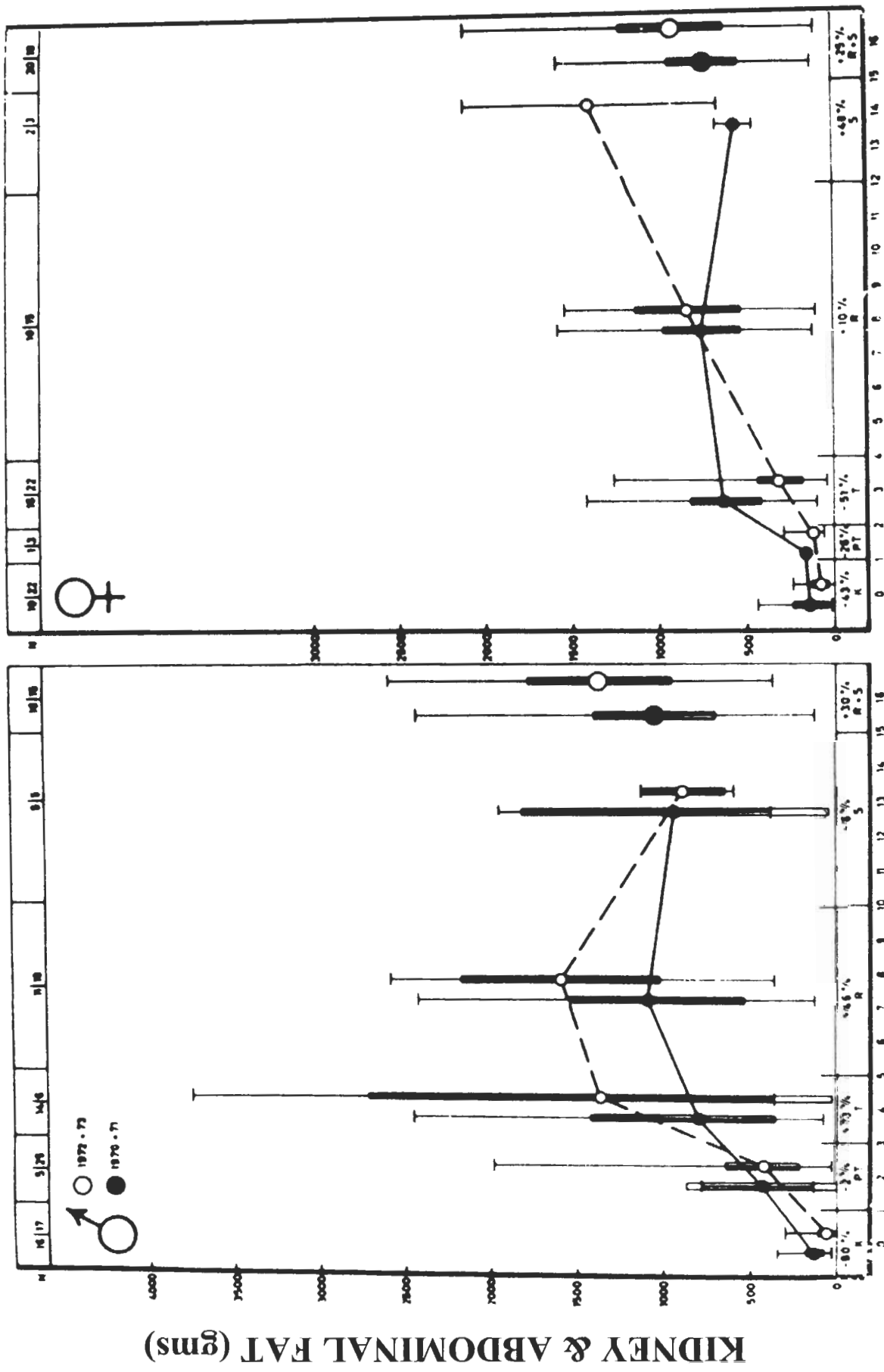


Fig. 6. Heart weight relative to age ● 1970+1971 vs. ○ 1972+1973.



### AGE (years) & CLASS

Fig. 7. Fat weight relative to age ● 1970+1971 vs. ○ 1972+1973.

should also consider other visceral fat besides that adhering to the kidneys or stomach mesentery; we should consider both the amount fat and its quality (e.g., kcal/kg).

Presumably, there is less seasonal variation in head weight and heart weight than in body weight. Thus, as an indicator of actual improvements in the chamois from 1970+71 to 1972+73, we consider head and heart weight most reliable. It is possible that if all biases due to seasonal changes in body weight could be eliminated from the data, that the plot for body fat (including subcutaneous and intramuscular fat) weight would even more closely resemble the plots for head and heart weights. On the other hand, body weight should be more rapidly sensitive to changes in environmental conditions, such as nutrition, weather, population density, social structure, etc.

### DISCUSSION

In order to interpret the foregoing comparisons of weights of the body, head, and heart, let us hypothesize that those parameters can be influenced by a variety of environmental factors, including:

- 1) nutrition
- 2) pathogens (parasites and disease)
- 3) weather
- 4) population density
- 5) population infrastructure (imbalanced maturity/age-sex ratios)

#### Nutrition

Although we have no data on nutritional value of plants eaten by our chamois, there is no reason to think that it has increased markedly during the years 1970-73. In fact, the habitat appears to be deteriorating (H. Kuen, pers. comm.).

Density of our chamois apparently declined <25% in the 1969/70 winter. This *might* have made more food available per capita to the survivors during subsequent years. If so, we would have expected any such change in nutritional status to be manifested by a more-or-less uniform increase in body weight for all ages of both sexes. Instead, the weight increases observed were consistently fully significant only for *mature* bucks and consistently *marginally* significant only for *adolescent* bucks.

#### Pathogens

Cursory study of our data on pathogens indicates a marked decrease in intensity of infestation by both liver flukes and lungworm. This appears to be a general decline for both sexes and all maturity-classes. If formal analysis of the data confirms this impression, we would tend to attribute the decline in infestation mostly to decreased population density and milder winters as of 1970 -- since these factors presumably affect all classes of chamois more-or-less equally (see below). Even if, however, analysis reveals that parasitism declined more for *mature* and *adolescent* bucks than for younger males or for females, one would not be justified in interpreting that as a *cause* of increased body weights for those bucks, rather than as a co-effect of some other factor, unless one could demonstrate why *mature* and *adolescent* bucks were particularly less likely to become infected than their peers.<sup>7</sup>

#### Weather

There is no obvious correspondence between the data presented for snow depth and air temperature versus mean body weight of chamois during the next autumn (Aug.-Dec.). It remains to be seen whether analyses of these parameters for the actual locations where chamois are living reveal such a relationship. Certainly, we would expect to find one.

It should be kept in mind that snow-crust strength also plays an important role in impacts by winter weather. Crust hinders attempts to dig for food under snow, but can facilitate travel over the snow.

The frequency of avalanches is also important, both in terms of danger to the chamois, and as a major mechanism that removes snow, opening potential feeding areas.

Furthermore, not only monthly mean weather values, but also variability should be considered. But whatever the relationships between meteorological parameters and severity of winters for the chamois *in general*, we must also question how differences in severity would tend to influence weight gain or loss in each maturity-sex class. We cannot expect changes in snow depth, crust strength, etc. to influence all chamois alike. For instance, a crust strong enough to support a *kid* is not necessarily strong enough to support a *mature*. Nevertheless, without detailed knowledge of these considerations, we see no basis for suspecting that changes in winter weather have been critical for *adolescent* and *mature* bucks, but not for younger males or for females. The problem is all the more puzzling when one recalls the high correspondence between snow depth and air temperature versus number of winter-kills found. Perhaps most of these chamois were killed by avalanches, rather than by exposure or starvation. Or, number of winter-kills found may be less a reflection of how many died, than of where and how they died (e.g., killed by avalanches). Colder, snowier winters may tend to concentrate chamois in locations (mainly ravines) where bodies are more easily found. Bodies buried under snow would be more likely than exposed remains to escape notice of scavengers (mainly ravens; occasionally fox or badger) until spring, when our game keepers scout the estate for dead animals. Each of these hypotheses will be tested in our future work.

### Population Density

Density is most appropriately addressed from the perspective of a specific group of animals (e.g., the entire population, or a particular maturity-sex class) in relation to a particular environmental parameter. Both per capita food availability and degree of parasitism, for instance, *might* be functions of the total number of chamois per unit area of feeding habitat -- although influences by red deer, roe deer, cattle, and other grazers and hosts should also be taken into account. But we would expect agonistic stress among *adolescent* and *mature* bucks to be much more strongly related to density of individuals within these classes than to density of the *residation* as a whole.

As discussed earlier, *mature* and some *adolescent* bucks are *territorial* during the summer; those found on a given estate during early summer, when the censuses were made, tended to be seen there constantly for the next several months, except when driven to shelter by a storm or by the sun. However, in autumn, as summer *territories* are abandoned, many Achental-W bucks go to Bächental-E for rut. Thus, summer density of bucks ought to be analyzed separately for each estate. But, since we have little information on autumn and winter distributions, except knowledge that many bucks and some does with young go to Bächental-E, these 2 estates must be considered together for that time of year. Ideally, one might consider all of Achensee-NW as a unit; but we lack reliable census data from the other Achensee-NW estates.

For the sake of argument, let us assume that seasonal movements from Achental-W and Bächental-E tend mainly to redistribute chamois within these 2 estates. Let us consider autumn and winter first: The strong deficit of *mature* bucks due to poor hunting practices through 1969, accentuated by the severe 1969/70 winter, was in large part cured by shifting hunting pressures to young bucks and to females. The number of *mature* bucks increased during 1970-72. From 1971-74, the number of *adolescents* plus *mature* bucks appears to have been fairly



stable, although the relative proportion of *mature* bucks kept increasing for Achental-W and Bächental-E combined.

So, to the extent that strife is hypothetically directly dependent on density of *adolescent* and *mature* bucks *during rut*, agonistic strife should have increased from 1970 to 1971, but stabilized somewhat thereafter.

Now let us consider summer density of bucks in Achental-W. The number of *mature* bucks has doubled since 1971; the number of *adolescents* + *matures* has increased by one-third. (Meanwhile, net density for the entire *residation* [excluding *kids*] varied only  $\pm 4\%$ ). Therefore, to the extent that strife in Achental-W was dependent upon density of *adolescents* + *matures* in **summer**, when *territories* are formed and defended,<sup>7</sup> agonistic stress should have decreased. *That is exactly the opposite of what our data indicate.* So, we are led to 1 or more of 3 conclusions:

- 1) Density of *adolescent* + *mature* males decreased during 1970-74, contrary to what our census data indicate.
- 2) Stress is not density-dependent as hypothesized.
- 3) The tendency towards higher stress due to higher density of *adolescent* + *mature* bucks was counteracted by other changes -- perhaps to balancing the ratio of *adolescent* to *mature* bucks, and of *mature* bucks to fertile *mature* does.

This latter possibility is most consistent with our data, as explained below.

### Population Infrastructure

To test how well these data support Bubenik's hypothesis, let us begin by summarizing the changes in social infrastructure: Summer maturity-sex ratios in Achental-W progressed from being badly imbalanced at least since 1970, to fair balance by 1972 and good balance by 1974 -- except that we had what may be a surplus of males during the summer. While Bächental-E also had a moderately good maturity-class balance by 1972, it had a strong deficit of *mature* males versus fertile *mature* females through 1974 (relative to what Bubenik considered optimum). Nevertheless, during breeding season, dispersal of Achental-W chamois into Bächental-E probably minimized local sex ratio imbalances. It is doubtful whether serious sex- or maturity-class ratio imbalances existed during rut on either estate after 1971 or 1972. Information on neighboring estates in Achensee-NW is scanty, but does suggest that *on average*, an adequate sex ratio among *matures* had been achieved by 1972.

Even though some of the bucks and does shot in Achental-W during 1970-73 participated in rut on neighboring estates, it is not likely that many encountered social conditions much more or less imbalanced than on our estate. So for 1970+71 vs. 1972+73, comparisons of body mass, etc. would seem to be valid indicators of the relative effects of imbalanced vs. balanced social infrastructure on those parameters, and thus on excessive energy expenditures and other forms of social stress, and on unnatural selection pressures.

Accordingly, the *Natural Selective Management (NSM) Hypothesis* predicts that all other things being equal: During 1970 and possibly 1971, rut would have been prolonged through at least 2 estrus periods. But by 1972, the frequency of fertile does being bred during their first estrus should have *begun* increasing. Theoretically, such changes should have been detectable by

<sup>7</sup> The Selye (1974) *General Adaptation Syndrome* is stimulated by a wide variety of stressors, but not by pathogens. The GAS is typified by increasing susceptibility to pathogens, due to impairment of the immune system and inflammation mechanism. This syndrome has been found in a wide variety of mammals and other vertebrates; so it probably occurs in chamois. (Stringham 1980).

before-vs.-after comparisons of (1) how long rutting behavior continued past mid- or late-December; (2) how many males and females, of what ages, participated in the rut during each month; (3) number/proportion of *kids* born in each month, beginning with May; (4) mortality rate of *kids*; and (5) monthly mean number of Graffian follicles, corpora lutea and albicans, and embryos, per harvested female.

The *NSM Hypothesis* also predicts that agonistic stress should have *begun* decreasing by 1972. This should have been manifested in altered (1) frequency and intensity of agonistic interactions, especially in association with territory formation or defense, and with rut; (2) numbers and ages of rutting bucks; (3) frequency and severity of injuries from accidents incurred during agonistic activity, such as headlong chases down steep slopes, so common in chamois (see Krämer 1969); and perhaps (4) endocrine glands. Both shortening the rut and decreasing strife should be manifested in better condition of *adolescent* and *mature* bucks, as shown through greater body and fat weights, and in decreased maturation rate. On the otherhand, too little is known to predict how quickly changes in *mean* social infrastructure for Achental-W (and Bächental-E) would be reflected in those parameters. Chamois, we must assume, are creatures of habit. Their distribution within Achental-W and Bächental-E during summers and during the rut, as well as their rank and territorial relationships, and so on, which developed under badly disrupted social conditions, might not readjust immediately to the better maturity-sex class ratios. Nor need all parameters improve at the same rate.

We might expect to find some improvement among those 2-yr-old males that attempt to participate in territorial and rutting activities; but any such improvements would be difficult to detect without specific knowledge of which individuals were involved. Decreased resource consumption by *adolescent* and *mature* bucks, and decreasing agonistic strife among them might eventually benefit young males, and benefit all females. But we would not expect to be able to detect such benefits by changes in body weight, etc. for these classes as soon as for *adolescent* and *mature* bucks. In fact, the only quickly detectable way in which improved harvest practices since 1970 would have benefited breeding females is that we shoot more *kids*, and thus reduce lactation costs for their dams.<sup>8</sup> This is done primarily where the *kid* is in poor condition, late-born, or retarded in its maturation -- and thus presumably has little chance of survival. If a doe is going to lose her *kid* anyway, better that she lose it early, before she has invested a great deal of her own resources in it -- which might jeopardize her own survival.

Field observations were made, mainly by Bubenik's student P. Meile and secondarily by our game keepers, to check length of rut and degree of agonistic strife. But so far data are insufficient to draw conclusions. Meile observed 1 instance of mating in winter 1971/72. As late as 1972, Bächental game keepers saw a couple of newborn *kids* (umbilical cord still attached) in September and October, indicating conception as late as March or April. Rutting activity was seen as late as mid-January in 1971/72, but not past late-December in 1973/74 or mid-December in 1974/75. But these are at best rough indicators that length of the rut decreased. Investigation and analysis of data on the other parameters is still underway.

Weight increases from 1970+71 to 1972+73 for body, head, and heart weights are fully significant ( $P < 0.05$ ) only for *mature* bucks. Only when the contrast is extended with data from another year, that is to 1970+71 vs. 1972-74, are weight increases also fully significant for

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<sup>8</sup> Balancing age-sex class ratios may have also reduced harassment of does by *adolescent* bucks, and thereby benefited the does. (Stringham 1980).

more direct human disturbance) could markedly decrease survival and reproductive success rates.

- 5) Excessive resource consumption, even at a moderate population density, could reduce carrying capacity of the habitat. The more resources each animal consumes, the fewer can be supported at a given level of nutritional status.

One key tactic of the *Natural Selective Management* strategy is to achieve and maintain a balance of maturity-sex classes such that the relationship between annual resource consumption vs. survival and reproductive success in each *residation* is optimized, so as to maximize the probability of long-term perpetuation of the metapopulation. Where predators have been decimated and cannot be reestablished, as in much of central Europe, it is sometimes necessary for humans to supplement remaining predation by highly selective hunting. A major goal of our research is to determine where supplementary harvest is critical for maintaining high quality of a population, and to learn how to select which individuals to shoot -- by determining age, maturity, social role, health, condition, etc. for the free-living animals. More broadly, thinking in terms of the entire ecosystem, our goal is to manage all component species of fauna and flora to achieve and maintain the ecological balances and *processes* vital to its long-term perpetuation. *Self-regulation* by the ecosystems is ideal. But where current or residual disruption by human influences prevents adequate self-regulation, managers must try to repair, or at least to compensate for the damages done. Embodied in the *NSM* concept of *regulation* is recognition that some fluctuation in any parameter (e.g., population density of ungulates) is natural and may play an important role in preserving the system; furthermore, ecological succession may be one of the processes that should be maintained.

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