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Relation of adrenal weight to sex, maturity and season in five species of small mammals

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The effect of sex, age, maturity, population density and season on the adrenal weight of five species of small mammals (*Sorex araneus, S. minutus, Clethrionomys glareolus, Ondatra zibethica* and *Microtus agrestis*) was studied in free-living populations in southern Finland. In sexually mature individuals the adrenal weight was greater in females; in immature animals the weight differed between the sexes only in *S. araneus,* in which the female adrenals were heavier. Sexual maturation clearly increased adrenal weight, except in male shrews. Adrenal weight correlated positively with body weight in immature animals, but this relationship was weakened by sexual maturation.

In most species the adrenal weight of immature individuals and mature males was fairly constant during the breeding season. In immature shrews, however, adrenal weight decreased continuously in both sexes from the July peak towards winter. In mature females of *C. glareolus* the adrenal weight was greatest in late summer. No differences in adrenal weight were observed between years. It is concluded that the reproductive state is one of the major factors affecting adrenal weight in these species.

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1. Introduction

Adrenal weight (mass) has been used as an index of social strife and social rank in small mammal populations (Christian 1950, 1980, Brenner et al. 1978, Bradley & Terman 1981). It has been suggested by Christian (1978) that the hypothalamo-pituitary-adrenal system has a central role in mediating the effect of psychogenic, socially induced (density-dependent) stress on the reproductive function of small mammals. There are, however, several factors which complicate the use of adrenal weight as an index of social strife. Firstly, there seem to be considerable species-specific differences in the degree of adrenocortical hypertrophy in response to stress (Christian 1980). Secondly, several other factors besides stress (e.g. sexual activity and sex) are known to affect adrenal weight in mammals (Sealander 1967). We therefore considered it important to study the effect of sex, age, reproductive state, population density and season on the adrenal weight of 5 species of small mammals.

Table 1. The numbers of small mammals used in the study (Lohja 1977-80). Years of high population level (see Pankakoski 1979) are in italics.

	1977	1978	1979	1980	Total
Sorex araneus (L.)		112	*218*	13	343
S. minutus (L.)		24	29	10	63
Clethrionomys glareolus (Schreb.)	*81*	103			184
Ondatra zibethica (L.)		48	98		146
Microtus agrestis (L.)	*125*	21			146

2. Material and methods

A total of 882 individuals belonging to five species of small mammals (Table 1) were collected from Lohja (60°15′N, 24°00′E), a district in southern Finland. The muskrats were collected from Lake Lohjanjärvi by local trappers and the skinned carcasses were stored in a deep-freeze (Pankakoski 1980). Most of the muskrats were trapped between April 15 and May 15. The other species were trapped on Jalassaari, an island (3.7 km^2) in Lake Lohjanjärvi, with cone traps (Pankakoski 1979) and occasionally also with snap traps. Trapping was carried out in 3-5-day periods, at approximately one month intervals from April to November. The small mammals drowned in the cone traps were dried, put in plastic bags and deep-frozen.

The age and reproductive status of the animals were evaluated according to the following principles:

The age of *C. glareolus* and *O. zibethica* was determined from the molar wear (Tupikova et al. 1968, Pankakoski 1980). The shrews (*Sorex*) were classified into overwintered and current-year individuals according to tooth wear and the colour and condition of their pelage (Crowcroft 1957). In *M. agrestis* mature females were classified as adults and juveniles according to the stage of the adult moult. Juveniles are individuals in juvenile pelage or at the start of the change to the first adult pelage (absolute age less than 30-35 days, Myllymäki et al. 1971, Myllymäki 1977).

The presence or absence of spermatozoa in the microscopical sperm test (Myllymäki et al. 1971) was the primary criterion used when classifying males as immature or mature. In some clear-cut cases, when the testes were small (*C. glareolus* and *M. agrestis* < 5 mm, *Sorex* < 3 mm) and the cauda epididymidis had no visible tubules, the males were classified as immature without the sperm test. In females the criteria were the diameter of the uterus horns, the number of visible embryos, the presence of placental scars and the state of lactation. The functional stage of the ovaries in female muskrats and shrews was studied under a binocular microscope; in *C. glareolus* and *M. agrestis* this was done only in uncertain cases. The animals were classified into groups according to their reproductive status: (1) immature individuals, (2) mature individuals: males with spermatozoa, females either pregnant (visible embryos, corpora lutea in the ovaries) or lactating, and (3) postreproductive individuals (only in female *C. glareolus*): with signs of earlier reproduction, i.e. placental and luteal scars (corpora albicantia) and decreasing mammary gland tissue. Females trapped just before the start of their first pregnancy in spring, with large Graafian follicles in the ovaries, were also classified as mature.

The skinned carcasses of *O. zibethica* were weighed to an accuracy of 5 g. Other species were weighed with a "Pesola" spring-scale (three types: capacities of 10, 30 and 100 g, using the most accurate scale for each animal).

The adrenal glands were dissected and kept in a solution of 0.2 M phosphate buffer (pH 7.2) until weighing, for a few hours at most. The adrenals were weighed with an analysis balance to an accuracy of 0.1 mg. Just before weighing, the adrenal gland was dried with absorbent paper. In most cases only one adrenal was weighed; if both adrenals were weighed (as was usually done in *S. minutus*), the mean of the two was used in later calculations.

The adrenal weights for *S. minutus* cannot be considered to be as accurate as in the other species, since the adrenal glands in this species are very small and this tends to increase quantitative errors during dissection. Moreover, the accuracy of the balance is not really satisfactory for *S. minutus*.

Arcsin transformation (Sokal & Rohlf 1969) was used when the relative adrenal weights (adrenal weight / body weight) were compared by statistical methods (Student's *t*-test, analysis of variance with Student-Newman-Keuls method for "a posteriori" comparisons of groups).

Table 2. Absolute and relative weights of adrenal gland and body weight (mean ± *SE*) in reproductive categories of five species of small mammals. In mature *Sorex* only overwintered individuals are included. The body weight of *O. zibethica* is the skinned carcass weight.

	n	(A) Weight of adrenal gland (mg)	(B) Body weight (g)	(Ratio A / B) Relative adrenal weight
S. araneus				
Mature ♂	71	2.48±0.068	11.70±0.125	0.214±0.0066
Mature ♀	26	4.38±0.232	12.27±0.342	0.363±0.0202
Immature ♂	118	2.73±0.059	7.87±0.054	0.347±0.0071
Immature ♀	117	2.98±0.066	7.90±0.049	0.377±0.0075
S. minutus				
Mature ♂	8	1.07±0.112	4.39±0.091	0.245±0.0255
Mature ♀	5	1.75±0.206	4.92±0.413	0.363±0.0454
Immature ♂	32	0.98±0.050	3.12±0.046	0.315±0.0162
Immature ♀	15	0.95±0.085	3.07±0.056	0.305±0.0246
C. glareolus				
Mature ♂	44	3.86±0.134	21.4±0.44	0.181±0.0056
Mature ♀	38	8.85±0.418	25.4±0.84	0.361±0.0213
Postreprod. ♀	6	3.98±0.271	19.9±0.84	0.200±0.0112
Immature ♂	60	2.48±0.087	15.2±0.28	0.163±0.0045
Immature ♀	36	2.35±0.093	15.0±0.36	0.157±0.0050
O. zibethica				
Mature ♂	83	145.0± 3.41	986 ±14.4	0.149±0.0038
Mature ♀	50	376.4±14.07	930 ±21.5	0.409±0.0152
Immature ♂	5	78.7±16.03	500 ±62.0	0.151±0.0129
Immature ♀	8	85.9± 9.07	557 ±39.0	0.154±0.0115
M. agrestis				
Mature ♂	43	4.83±0.190	40.5±1.75	0.125±0.0052
Mature ♀ Ad.	29	6.71±0.362	31.4±1.41	0.215±0.0087
Mature ♀ Juv.	5	3.52±0.745	17.8±1.29	0.194±0.0324
Immature ♂	38	4.05±0.161	21.3±0.44	0.191±0.0072
Immature ♀	31	3.90±0.182	19.6±0.50	0.200±0.0078

3. Results

The absolute and relative adrenal weights and the body weights of the reproductive categories are presented in Table 2.

3.1. Effect of sex and maturation

In all the species the adrenal weight (both absolute and relative) is greater in mature females than mature males (Table 3). The difference between sexes is greatest in *O. zibethica* and *C. glareolus*. The immature animals usually show no difference between the sexes: the ratio ♀/♂ is near 1 (Table 3). In immature *S. araneus*, how-

Table 3. Effect of sex and maturation on the adrenal weight ratio (♀/♂ and mature/immature) of five species of small mammals. For actual means, see Table 2. Statistical significance was tested by Student's *t*-test (ns = not significant, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

	Sex		Maturation	
	Mature ♀/♂	Immature ♀/♂	Males (M/I)	Females (M/I)
Relative adrenal weight ratio				
S. araneus	1,7***	1.1**	0.6***	1.0 ns
S. minutus	1.5*	1.0 ns	0.8 ns	1.2 ns
C. glareolus	2.0***	1.0 ns	1.1*	2.3***
O. zibethica	2.8***	1.0 ns	1.0 ns	2.7***
M. agrestis	1.7***	1.0 ns	0.7***	1.1 ns
Absolute adrenal weight ratio				
S. araneus	1.8***	1.1**	0.9**	1.5***
S. minutus	1.6**	1.0 ns	1.1 ns	1.8***
C. glareolus	2.3***	1.0 ns	1.6***	3.8***
O. zibethica	2.6***	1.1 ns	1.8***	4.4***
M. agrestis	1.4***	1.0 ns	1.2**	1.7***

ever, the adrenals of the females are heavier.

The sexual maturation of small mammals is usually accompanied by adrenal growth (Table 3). Although the difference in the absolute adrenal weights of immature and mature individuals is usually distinct, the increase in the relative adrenal weight depends on the species and sex (Table 3). In *C. glareolus* the effect of maturation is clear in both sexes. In *O. zibethica* a clear difference in the relative adrenal weights between mature and immature animals is seen only in the females. The increase of adrenal weight due to maturation is smaller in *M. agrestis, S. araneus* and *S. minutus*. The relative adrenal weights of these three species are about the same in mature and immature females; in males the relative weight (in *S. araneus* even the absolute value) is greater in immature than mature animals.

Contrary to the situation in voles, usually only a small percentage of young female shrews mature during their first summer; most of the females and all the males of *S. araneus* and *S. minutus* remain immature until the next spring (Pucek 1960). In the females of both shrews and *C. glareolus* sexual maturation raises the adrenal weight to a certain level, which seems to be independent of age (Table 4). On the other hand, the overwintered and current-year cohorts of *S. araneus* and *C. glareolus* differ significantly in size and consequently also in relative adrenal weight (Table 4). The same tendency is seen in the scanty material of *S. minutus*.

3.2. Effect of pregnancy

Only in *O. zibethica* did the adrenal weight of visibly pregnant females differ statistically significantly from the value of other mature females (invisible pregnancy or lactation stage; Table 5), being greater in the visibly pregnant females. The opposite tendency is evident — although not statistically significant — in all the other species in Table 5. The reason for this clear difference in *O. zibethica* is most probably the fact that in that species only the first pregnancy of the female is concerned (spring material). The females of *O. zibethica* mature during April and the first visibly pregnant females were trapped in May. The adrenals are still growing during April and May (Fig. 1).

Table 4. Comparison of adrenal and body weight (mean ± *SE* and *n*) between overwintered and current-year cohorts of mature females of *S. araneus*, *S. minutus* and *C. glareolus*.

	Overwintered	Current-year	Difference t
Adrenal weight (mg)			
S. araneus	4.38±0.232 (26)	4.25±0.310 (11)	0.309 ns
S. minutus	1.75±0.206 (5)	1.33±0.073 (3)	1.485 ns
C. glareolus	8.08±0.511 (18)	9.54±0.620 (20)	1.783 ns
Body weight (g)			
S. araneus	12.3±0.34 (26)	9.5±0.41 (11)	4.614***
S. minutus	4.9±0.41 (5)	4.0±0.40 (3)	1.478 ns
C. glareolus	28.2±1.18 (18)	22.9±0.89 (20)	3.643***
Relative adrenal weigh			
S. araneus	0.36±0.020 (26)	0.44±0.025 (11)	2.336*
S. minutus	0.36±0.045 (5)	0.34±0.039 (3)	0.319 ns
C. glareolus	0.29±0.017 (18)	0.43±0.031 (20)	3.757***

Table 5. Effect of pregnancy on adrenal weight (mean ± *SE* and *n*). Only absolute adrenal weights are used, since pregnancy increases body weight and this affects the relative values.

	Adrenal weight (mg)		
	Visibly pregnant females	Other mature females	t-test
S. araneus	4.1±0.24 (15)	4.5±0.27 (22)	1.10 ns
S. minutus	1.5±0.18 (5)	1.7±0.29 (3)	0.71 ns
C. glareolus	8.8±0.55 (24)	9.1±0.64 (14)	0.31 ns
O. zibethica	441±30.0 (14)	356±13.6 (38)	2.95**
M. agrestis	6.7±0.57 (13)	7.1±0.46 (14)	0.52 ns

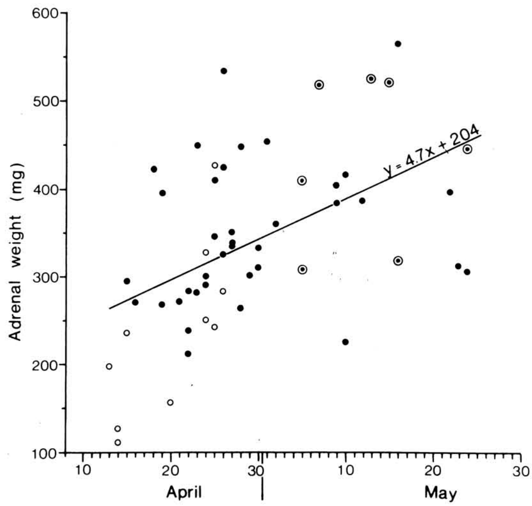

Fig. 1. The increase in adrenal weight of female *O. zibethica* (< 1 yr. old) in spring. Open circles = females maturing, but without Graafian follicles or corpora lutea in ovaries; closed circles = mature females, not visibly pregnant; closed circles with outer rings = visibly pregnant females. The regression analysis ($F = 16.22$***): x = date of trapping (April 1 = 1), y = adrenal weight (mg).

Table 6. Correlation coefficients (r) between adrenal weight and body weight in five species of small mammals. Numbers of animals in parentheses. Juvenile mature females of *M. agrestis* and current-year mature females of *Sorex* are excluded. In *O. zibethica* the weight of the skinned carcass used.

	Mature ♂♂	Mature ♀♀	Immature
S. araneus	+0.149 ns (68)	+0.168 ns (24)	+0.391***(230)
S. minutus	+0.437 ns (12)		+0.368* (38)
C. glareolus	+0.363* (42)	+0.080 ns (36)	+0.566*** (96)
O. zibethica	+0.274* (83)	+0.310* (43)	+0.835*** (13)
M. agrestis	+0.586*** (41)	+0.672*** (27)	+0.413*** (69)

Table 7. Partial correlation coefficients (r) between adrenal weight of *O. zibethica* and age and body weight of the animal (skinned carcass weight). Mature individuals from the spring sample, immature animals from summer and autumn trappings.

	Mature ♂♂	Mature ♀♀	Immature
Age	+0.362***	+0.141 ns	+0.177 ns
Body weight	+0.237*	+0.239 ns	+0.592*
n	83	43	13

3.3. Adrenal weight and body weight

As could be expected, the adrenal weight correlates positively with the body weight in small mammals (Table 6). This relationship is clear in immature animals, but in mature individuals there are differences between species. The correlation is highest in mature *M. agrestis* and lowest in mature *S. araneus* and female *C. glareolus*. Basically, the adrenal weight grows linearly with body weight, but sexual maturation often causes divergences from this trend.

In *O. zibethica* the relationships between the animal's age, body weight and adrenal weight were studied by calculating partial correlation coefficients (Sokal & Rohlf 1969: 540) between the three variables (Table 7). In mature males of *O. zibethica* the adrenal weight is positively correlated with body weight and age, especially the latter. On the other hand in mature females the correlations are low. The adrenal weight of mature females is thus affected by some other factor(s), the most evident of these being the reproductive stage of the female (cf. connections with the trapping time, Fig. 1). In immature muskrats the adrenal weight is correlated with body weight, but not with the age of the animal.

3.4. Annual and seasonal changes in adrenal weight

In some cases there was not sufficient material in each reproductive category for temporal comparisons. Comparisons between years were performed only in *S. araneus* (comparable trapping periods in 1978–79) and *M. agrestis* (pooled data for mature males in 1977–78), both of which showed no differences in adrenal weight. However, the mature males of *M. agrestis* were heavier during the peak (1977) than the low (1978) phase and as a result there is a statistically significant difference in the relative adrenal weight (Table 8).

The monthly changes in the relative adrenal weights of *S. araneus, C. glareolus* and *M. agrestis* are presented in Figures 2–4. The absolute adrenal weights would show largely similar trends. Because of the differences between years in the relative adrenal weight of *M. agrestis*, the monthly comparisons for this species were made only in the peak year (1977).

After the drop in spring the relative adrenal weight of mature males and females of *S. araneus* seems to increase through the reproductive season towards the autumn (Fig. 2). This increase is not statistically significant, however. The decline in the relative adrenal weight (significant in males) from April to May is explained by the increase in body weight during this time (Pucek 1960, 1965). The April mean for the absolute adrenal weight does not differ from the later ones. The numbers of mature *S. minutus* in the monthly trappings are not sufficient for statistical treatment.

In both sexes of immature *S. araneus* the adrenal weight reaches its maximum in July, after which it decreases gradually towards the winter (Fig. 2). This decrease is statistically significant in both sexes, and it is also seen in absolute weights of the adrenal gland. The same tendency is found in immature males of *S. minutus:* adrenal weight decreases from July onwards ($F = 10.06$***).

In *C. glareolus* and *M. agrestis* the adrenal weight of immature individuals and mature males is fairly stable during the whole season (Fig. 3 and 4). In mature females of the two species it shows distinct differences between the months. The adrenal weight grows continuously during the reproductive season and reaches its peak in

Table 8. Comparison of adrenal (mg) and body weights (g) (mean ± SE and n) of mature males of *M. agrestis* in peak (1977) and low (1978) phases of population cycle.

Weight	Peak phase	Low phase	t-test
Adrenal	5.04 ±0.249 (30)	4.46 ±0.186 (8)	1.17 ns
Body	45.6 ±1.75 (30)	28.6 ±0.196 (8)	4.75***
Rel. adrenal	0.109 ±0.0057 (30)	0.160±0.0116 (8)	4.44***

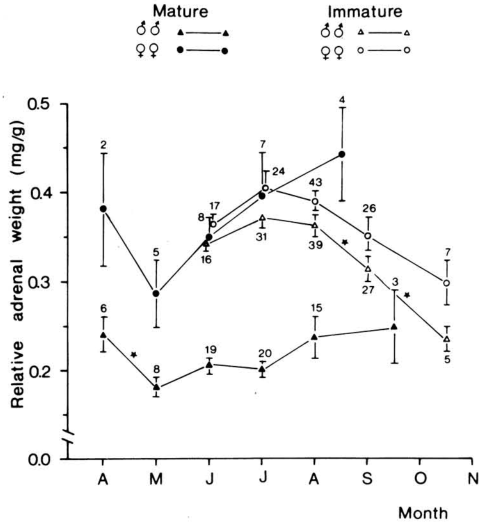

Fig. 2. Seasonal changes in the relative adrenal weight of *S. araneus* (mean $\pm SE$). Analysis of variance between the months: mature males $F = 2.53$*, mature females (overwintered) $F = 1.94$ ns, immature males $F = 6.36$***, immature females $F = 3.75$**. Statistically significant differences between the means of consecutive trapping months are marked with asterisks (Student-Newman-Keuls method).

August. After this a decline is evident in *C. glareolus*; the postreproductive females in the autumn samples have an even more reduced adrenal weight (Fig. 3). Mature *M. agrestis* females are lacking in the autumn material 1977, so that a decline in adrenal weight cannot be demonstrated (Fig. 4).

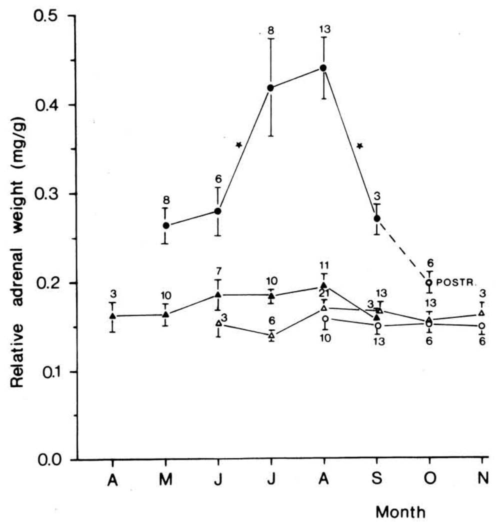

Fig. 3. Seasonal changes in the relative adrenal weight of *C. glareolus* (mean $\pm$ *SE*). Analysis of variance between the months: mature males $F = 1.34$ ns, mature females (postreproductive individuals excluded) $F = 5.57$**, immature males $F = 1.63$ ns, immature females $F = 0.04$ ns. The adrenal weight of the six postreproductive females is the mean of two females from each of the months Sept., Oct., Nov. For symbols, see Fig. 2.

When relative adrenal weights are used, the results are affected by changes in the population structure, because young mature females have greater relative values (see Table 4). In *C. glareolus* a complete turn-over of the individuals in the category of mature females was observed during the summer. (Until June this group consisted merely of overwintered individuals; in July and August 63 % and 92 %, respectively, consisted of current-year individuals, and in the autumn all the mature and postreproductive females had been born during the current year.) The population structure of *M. agrestis* had most probably changed in a similar way (Myllymäki 1977), although this was not verified in the present study. However, the same tendency (peak in August) is evident also in the absolute adrenal weights of mature females in the two vole species. The differences between the trapping months are significant in *C. glareolus* ($F = 5.08$**), but not in *M. agrestis* ($F = 1.72$ ns) in absolute values.

4. Discussion

The sexual dimorphism in the adrenal weight of sexually active animals in all the species investigated is in agreement with previous studies (Pucek 1965, Chitty & Clarke 1963, Chitty 1961, Schacher & Pelton 1976, Gustafsson & Anderson 1980). *S. araneus* was the only species in which there was also significant dimorphism in the adrenal weights of immature animals. This is in accordance with the results of Siuda (1964), who

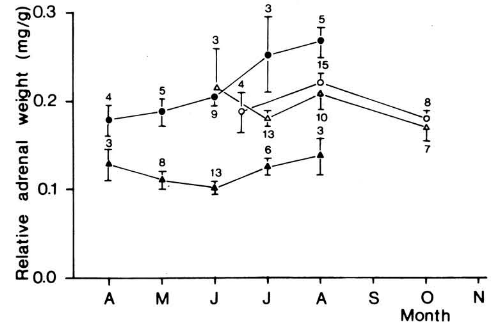

Fig 4. Seasonal changes in the relative adrenal weight of *M. agrestis* (mean $\pm SE$). Analysis of variance between the months: mature males $F = 2.64$ ns, mature females (adults) $F = 6.43$**, immature males $F = 1.28$ ns, immature females $F = 3.19$ ns. For symbols, see Fig. 2.

noted sex-specific differences in the width of the inner cortical zones in immature *S. araneus*. Adrenal weight seems to differ between the sexes in many other species of small mammals as well: *C. rutilus* (Sealander 1967), *C. rufocanus* (Wallgren et al., unpublished), *P. maniculatus* (McKeever 1964, *M. arvalis* (Delost 1952) and *S. hispidus* (Negus et al. 1961) etc.

With the exception of *Mesocricetus auratus* (Zieger et al. 1974) the adrenals of females are usually heavier. These sex differences are partly due to the differential effects of androgens and oestrogens on the adrenal cortex (Asari et al. 1979, Rodgers et al. 1974) and partly to the effects of these hormones on pituitary function (Rodgers et al. 1974). The histomorphological basis of this dimorphism resides in the innermost zones of the cortex zona fasciculata, zona reticularis and X zone, which are more developed in females. Many microtines have an additional juxtamedullary layer, the X zone, which is morphologically distinct from the zona reticularis. In immature animals of both sexes the X zone is present as a narrow zone surrounding the medulla. During sexual maturation and pregnancy it usually hypertrophies in females. In males the X zone generally involutes during puberty, probably owing to the action of androgens (Howard-Miller 1927, Chester Jones 1949, Delost 1952, Delost & Delost 1954, Chitty & Clarke 1963, Siuda 1973). However, the effect of pregnancy and sexual maturation on the structure of the X zone varies considerably between and within species (Delost 1952, 1957, Chitty & Clarke 1963, Vinson & Chester Jones 1963, Christian & Davis 1964, Siuda 1964). Unlike the zona fasciculata and zona reticularis, which are known to be dependent on ACTH, the X zone is thought to be dependent on the trophic influence of pituitary gonadotrophins, mainly LH (Chester Jones 1949, Siuda 1973). However, the physiological significance of this juxtamedullary zone, histochemically different in many respects from the other cortical zones (Chester Jones 1949, Rubin et al. 1963, Tähkä 1979), remains enigmatic.

In this study the sexual dimorphism in adrenal weight was most pronounced during the summer months, the period of maximum reproductive activity, and declined in the autumn, at least in *C. glareolus*. Since the presence of an X zone has been demonstrated previously in *C. glareolus, M. agrestis* and *S. araneus* Delost & Delost 1954, Chitty & Clarke 1963, Siuda 1964, 1973), these changes were probably due to the hypertrophy and subsequent involution of the inner cortical zones brought about by seasonal changes in the synthesis of pituitary gonadotrophins and gonadal oestrogens and androgens (Chester Jones 1949, Siuda 1964, 1973, Hyvärinen 1969, Rodgers et al. 1974, Clarke 1977). The reproductive state is one of the major factors affecting the adrenal weight in seasonally breeding rodents (Sealander 1967, Chitty & Clarke 1963). However, the tendency of the adrenal weight in mature *C. glareolus* females to increase during the breeding season is hard to explain by adreno-gonadal interactions and/or by changes in population structure. It has been demonstrated, at least in *M. agrestis*, that there is no cumulative effect of successive pregnancies on adrenal weight (Chitty & Clarke 1963).

In *S. araneus* and *S. minutus* statistically significant seasonal changes in the adrenal weight were noted in immature animals as well. The decline in the adrenal weight of immature males and females in the autumn, as also the reduction in adrenal size observed in *S. araneus* by Hyvärinen (1969), may reflect the decline in gonadal weight known to take place at this time of the year (Pucek 1960). It might also be the consequence of a decline in social agonistic interactions in the population. The latter explanation is supported by the studies of Croin Michielsen (1966) and Hawes (1977), who observed strict territoriality in immature individuals of *Sorex* species. According to Hawes (1977) the mortality of immature animals was greatest during the summer, when territories are being established.

In *O. zibethica* seasonal changes could not be studied, since only spring material was available. According to Beer & Meyer (1951) and Schacher & Pelton (1976), maximum adrenal weights are reached in the autumn after the cessation of the breeding season. Clearly some other factor(s) besides the reproductive state affects seasonal changes in adrenal weight in this species. However, the spring increase in the adrenal weight of female muskrats noted by Beer & Meyer (1951), Schacher & Pelton (1976) and the present authors is probably due to the onset of breeding.

In *M. agrestis, C. glareolus, S. araneus* and many other eutherian mammals as well, adrenal weight and cortical width have been shown to increase during pregnancy (Chitty & Clarke 1963, Siuda 1964, 1973, Jorne-Safriel 1968). Evidence has been accumulated which indicates that the initiation of the adrenal growth associated with pregnancy is triggered directly by mating, without ovarian involvement (Gustafsson & Anderson 1980). The contradictory results obtained in this study are due to the fact that the animals were usually trapped throughout the breeding season and thus formed a heterogeneous collection of nulli-, uni- and multiparous individuals. Only a fraction of the mature females classified as "not visibly pregnant" were thus nonpregnant and nulliparous, the others being nonpregnant and uni- or multiparous, or in the early stages of pregnancy and/or lactating. In *O. zibethica*, in which pregnancy was observed to have a statistically significant effect on adrenal weight, the situation was different, since only spring material was used and thus a large portion of the animals classified as "not visibly pregnant" were nulliparous virgin females.

Our scanty data do not support the idea that adrenal weight depends on the phase of the population cycle. The fact that the relative adrenal weight of mature *M. agrestis* males was smaller in the peak year than in the low phase is explained by the difference in the age (and consequently in the size), at which the voles reach sexual maturity (Kalela 1957, Myllymäki 1977).

The extent to which adrenal enlargement may be due to hostile social interactions is hard to assess, since such changes may very well be masked by the marked influence of the reproductive state on adrenal weight. Furthermore, in some species adrenal weight is not a reliable index of adrenocortical function (Christian 1980). However, according to Chitty & Clarke (1963), the strong positive correlation between body weight and adrenal weight in mature *M. agrestis*, also observed in the present study, may reflect the effect of social interactions.

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