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EFFECT OF TEMPERATURE ON SURVIVAL DURING THE FIRST MONTH OF LIFE IN THE FIELD VOLE, *MICROTUS ARVALIS*, RAISED UNDER DIFFERENT CONDITIONS OF DAYLIGHT RATIO AND FEEDING

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SUMMARY

The temperature at which field-vole pups are raised plays a principal role in their survival during the first month of life. Mortality rise as the temperature drops, is explained by inefficient thermoregulation at weaning.

The quality of the alfalfa eaten also affects survival, *i.e.* alfalfa harvested at an early stage of vegetation in the spring enhances the chances of survival of the pups more than alfafa harvested at a later stage of vegetation in the fall.

Daylight ratio does not affect survival from birth to 30 days.

Low temperature and fall alfalfa, the two factors unfavorable to survival, may partially explain the mortality rates observed in nature during the first months of life.

At the present time it is impossible to directly measure mortality rate during the first month of life in natural field-vole populations because these animals cannot be captured. Ecologists must thus use indirect methods (SPITZ, 1974). However, the juvenile population within herbivorous small rodent populations is very high. KREBS *et al.* (1969) estimate that only 20 p. 100 of young *Microtus pennsylvanicus* or *Microtus ochrogaster* survive between birth and one month. In *Microtus arvalis* mortality rates range between 40 and 90 p. 100 during the year (MARTINET and SPITZ, 1971).

The effect of some environmental factors on juvenile mortality can be measured on animals in captivity. A previous study (MARTINET and MEUNIER, 1969) showed the importance of the feeding value of the vegetation eaten in relation to survival rate ; numerous other factors probably play a role, and that is why we have studied the effect of temperature associated to various stock-raising conditions.

MATERIAL AND METHODS

Animals

The female is given wood shavings and hay to make her nest. From the day of birth the cages containing the mothers and their pups are separated into different experimental groups. At 14 days the female is taken from the cage. The pups are thus weaned but may stay in the nest up to one month, at which time they are isolated in individual cages.

Experimental groups

Series 1.

Twelve groups of animals were constituted according to a 3 × 2 × 2 experimental design; they were raised under the following environmental conditions :

— three temperatures : 5°C, 22°C or 33°C.

During the experiment temperatures varied in the first case between 3°C and 9°C, in the second case between 20°C and 25°C and in the third case between 28°C and 35°C.

— two diets : spring or summer alfalfa.

The alfalfa was cut at an early stage of growth (30 cm), either during the first vegetative cycle in April (spring alfalfa) or during the second vegetative cycle in June (summer alfalfa). It was ground and dried, then wetted again when distributed daily *ad libitum.* No other water was given.

— two daylight ratios : 15 h or 10 h of light per 24 h. Light level in the cages ranged between 200 and 300 lux.

Ambient humidity recorded throughout the experiment varied between 40 and 85 p. 100 at 5°C, between 30 and 75 p. 100 at 22°C, and between 40 and 45 p. 100 at 33°C.

Series 2.

Eight groups of animals were constituted according to a 2 × 2 × 2 experimental design and raised under the following environmental conditions :

— two temperatures : 5°C or 22°C. Fluctuations are the same as in series 1.

— two diets : spring or fall alfalfa. The alfalfa was cut, either at an early vegetative stage of growth (30 cm) during the first vegetation cycle in April (spring alfalfa) or at a later stage of growth (60 cm or preflowering) during the fourth vegetation cycle in October (fall alfalfa). In this series alfalfa was deep-frozen 15 minutes after harvesting and stored at — 18°C until utilization. It was given in the frozen state daily *ad libitum.*

— two daylight ratios : 15 h or 10 h of light per 24 h.

Series 3.

Eight groups identical to those of series 2 were constituted, but the pups were separated from the mother one week later, *i.e.* at 21 days instead of at 14 days.

Observations

The pups in each series were counted at birth and again at 7, 14, 21 and 30 days ; every day any dead animals were removed from the nests. Litters were weighed at 7, 14 and 21 days. In some cases, pups were weighed individually at 14 days.

Survival rates were compared using the χ^2 test.

RESULTS

The role of ambient temperature in the survival of the young depends on many factors which are analyzed successively.

1. — *Effect of age of animals*

During the first week mortality of the pups living at 5°C or at 22°C was the same ; it varied between 3 and 9 p. 100 in the first series (table 1), and between 7 and 29 p. 100 in the second series (table 2). In the first series mortality was the highest at 33°C, *i.e.* at 7 days 8 to 22 p. 100 of the pups were dead. The difference between the 33°C groups on one hand and the 5°C and 22°C groups on the other, was significant in 3 cases out of 4 (table 1).

During the second week mortality increased at 5°C. However, results varied from one group to another since there is 1 to 22 p. 100 mortality in series 1, and 20 to 34 p. 100 mortality in series 2.

TABLE I

Juvenile mortality rate during the first four weeks of life

Results are expressed in percentage of young dead at a given age as compared to those dead at the preceding age (series 1)

Daylight ratio	Diet	Temperature	Number born	Litter size	Mortality rate (in %) from 0 to 7 days	7 to 14 days	14 to 21 days	21 to 30 days
15 L : 9 D	Spring alfalfa	5°C	120	4.8	4	14*	77**	0
		22°C	155	4.4	4	0	23*	9
		33°C	156	4.1	8	4	2	0
	Summer alfalfa	5°C	166	5.2	3	22**	76**	6
		22°C	115	4.3	4	1	37**	23*
		33°C	135	4.8	11*	1	7	6
10 L : 14 D	Spring alfalfa	5°C	164	4.1	9	3	12 (1)	26* (1)
		22°C	118	3.9	8	1	5	6
		33°C	133	4.8	22**	3	0	14
	Summer alfalfa	5°C	117	4.6	4	1	73**	19**
		22°C	91	4.3	4	3	13	0
		33°C	80	4.4	20**	0	24	0

* $P < 0.05$] Comparisons are made within the same group between 5°C and 21°C
** $P < 0.01$] and between 22°C and 33°C.

(1) Females of this group were given cellulose handkerchiefs for nest construction besides shavings and hay.

At 22°C and 33°C mortality is very low between 7 and 14 days ; at 22°C the high disappearance rates of the two groups fed fall alfalfa (table 2) are due to the feeding value of the alfalfa which is analyzed further on.

TABLE 2

Mortality rate of young during the first four weeks of life

Results are expressed in percentage of young dead at a given age as compared to those dead at the preceding age (series 2)

Daylight ratio	Diet	Temperature	Number born	Litter size	Mortality rate (in %) from 0 to 7 days	7 to 14 days	14 to 21 days	21 to 30 days
15 L : 9 D	Spring alfalfa	5°C	109	5.1	17	34**	51**	0
		22°C	86	5.3	7	3	12	11
	Fall alfalfa	5°C	116	5.2	29	28	63	26*
		22°C	142	4.7	27	29	62	0
10 L : 14 D	Spring alfalfa	5°C	83	4.9	16	32**	67	11
		22°C	52	5.3	9	3	43	4
	Fall alfalfa	5°C	103	4.8	26	20*	65*	62*
		22°C	143	4.9	29	40	33	48

* $P < 0.05$
** $P < 0.01$
Comparisons are made within the same group between temperatures.

From weaning on (after 14 days) there is considerable mortality in young raised at 5°C. Disappearance rates between 14 and 21 days vary between 51 and 77 p. 100 ; most of the animals die in the three days following weaning.

Mortality at 22°C, although lower than at 5°C, ranges between 5 and 73 p. 100 in the first series, between 12 and 62 p. 100 in the second one. At 33°C mortality rate does not exceed 24 p. 100 between 14 and 21 days.

After 21 days mortality decreases in all groups except two in which animals were fed fall alfalfa.

2. — *Effect of diet*

Survival rates during the first month are the same in the groups fed spring or summer alfalfa. However, a lower survival rate is observed ($P < 0.05$) in one case when summer alfalfa is given (table 3).

Fall alfalfa is very unfavorable to survival of the pups. The difference between spring and fall alfalfa is significant ($P < 0.01$) in the two 22°C groups. This unfavorable effect of fall alfalfa already appears in the first week of life (table 2).

3. — *Influence of daylight ratio*

No effect of the daylight ratio on the survival of young was observed.

TABLE 3

Mortality rate of young between 14 and 21 days in relation to weight at 14 days
(Weight of young is obtained by dividing litter weight by the number of young alive)

Daylight ratio	Diet	Temperature	Number of litters	Mean weight g ± S.E.	Mortality rate in p. 100
15 L : 9 D	Spring alfalfa	5°C	25	8.6 ± 0.7*	77*
		22°C	35	7.2 ± 0.3	23
		33°C	38	6.9 ± 0.2	2
	Summer alfalfa	5°C	32	7.4 ± 0.5*	76*
		22°C	23	6.2 ± 0.2	37
		33°C	23	6.2 ± 0.2	7
10 L : 14 D	Spring alfalfa	5°C	38	9.5 ± 0.4*	12 (1)
		22°C	30	8.9 ± 0.3	5
		33°C	26	7.4 ± 0.3	0
	Summer alfalfa	5°C	24	7.7 ± 0.3	73*
		22°C	21	8.2 ± 0.3	0
		33°C	18	7.3 ± 0.3	0

(1) Females of this group were given cellulose handkerchiefs for nest construction besides shavings and hay.

* $P < 0.01$ Comparisons are made within the same group between 5°C, 21°C and 33°C.

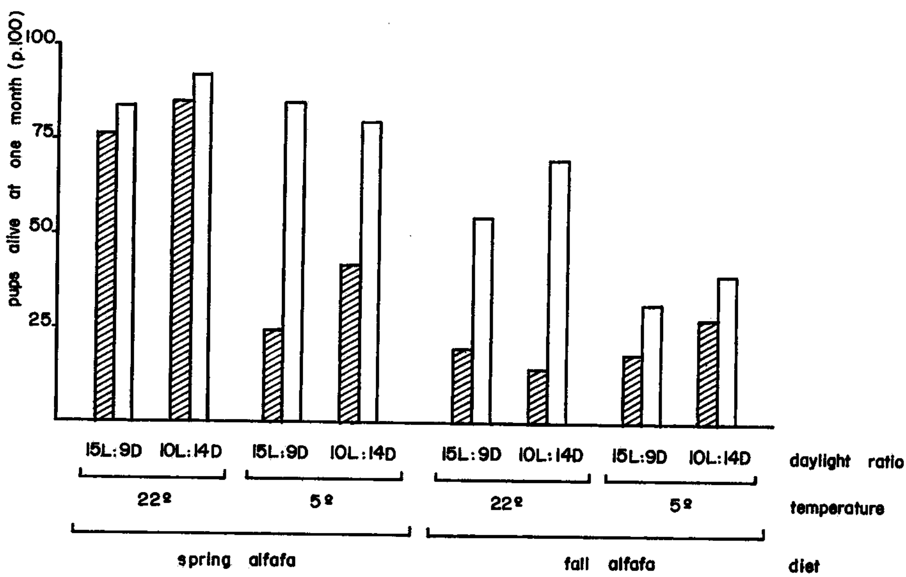

FIG. 1. — *Effect of age at weaning on survival of young*

Weaning at 14 days
Weaning at 21 days

4. — *Effect of age of pups at weaning*

Weaning at 21 days instead of at 14 days considerably improved future survival rate of the pups. Increase of survival rate is especially clear in animals raised at 22°C and fed fall alfalfa or raised at 5°C and fed spring alfalfa. In groups where both factors unfavorable to survival (5°C and fall alfalfa) are associated, mortality between 14 and 21 days remains high in spite of the maternal presence (text fig. 1).

5. — *Effect of weight of pups at weaning*

The weight of pups at weaning determines their future survival. The minimum weight necessary for survival increases when the temperature at which animals are raised decreases. This is shown by the following facts :

— survival rates after weaning are much better at 33°C than at 22°C or 5°C, while pups raised at 33°C are the smallest (table 3).

— at 22°C pups weighing at least 5 grams have a 50 to 80 p. 100 chance of surviving ; if raised at 5°C pups must weight more than 7.5 grams to have the same chance of surviving. At 33°C, where survival rates after weaning are always higher than 75 p. 100, there seems to be no relation between body weight and survival (table 4).

TABLE 4

Survival rate of young during the week following weaning in relation to weaning time
(Young were weighed individually)

Diet	Weight at 14 days in grams	Survival rate between 14 and 21 days	
		22°C	5°C
Spring alfalfa	⩽ 5	38	10
	5.1 to 7.5	80	6
	> 7.5	98	68
Fall alfalfa	⩽ 5	15	0
	5.1 to 7.5	50	0
	> 7.5	91	52

6. — *Effect of litter weight at weaning*

Whole litters dead between 14 and 21 days at 5°C and 22°C weigh on an average 6 grams less at 14 days than those totally surviving. The difference is not significant because of the wide variability in litter weight (6 to 54 grams). At 33°C very few litters disappear entirely after weaning (table 5).

The relation litter weight-future survival in terms of ambient temperature is much less clear than that of individual weight-survival.

TABLE 5

Effect of litter weight at weaning on future survival of the young
(61) Number of litters

Temperature	Litter weight at 14 days	
	Alive at 21 days	Dead at 21 days
5°C	32.4 ± 3.1 (61)	26.1 ± 2.1 (69)
22°C	32.0 ± 3.3 (108)	26.6 ± 1.8 (22)
33°C	24.9 ± 4.1 (131)	28.9 ± 4.3 (15)

7. — *Effect of litter size*

The number of young born per litter range from 1 to 6. Litter size does not seem to affect survival from birth to weaning or from weaning to one month. However, postweaning survival rate is higher in larger litters, probably because their weight is higher than that of the smaller litters.

8. — *Effect of nest quality*

In one of the 5°C groups of the first series, the addition of cellulose handerkerchiefs allowed the mothers to build more compact nests than when only shavings and hay were offered. An exceptional survival rate is thus noted after weaning, *i.e.* 77 p. 100 instead of 18 to 26 p. 100 (table 1).

On the contrary, at 33°C the mothers do not take care of the nest built before birth.

DISCUSSION

The survival of field-vole pups during the first month of life depends in a large part on ambient temperature ; the lower is the temperature, the higher is the mortality rate. The same phenomenon is observed in another vole, *Microtus ochrogaster*, (GIER and COOKSEY, 1967), rat (CHEVILLARD and CADOT, 1963) and mouse (BARNETT and MANLY, 1959).

Low mortality rate during the suckling period, the abrupt death of a large number of young following weaning and the relationship individual weight-temperature-mortality indicate that two thermoregulation systems are involved.

GEBCZYNSKI (1969) notes social thermoregulation in *Clethrionomys glareolus* ; animals in a group use less oxygen. The efficacy of this thermoregulation is related to group size and weight. The relationship observed here between litter weight-future survival and the effect of the withdrawal of the mother from the nest account for this first method of thermoregulation in *Microtus arvalis*.

However, in the field-vole individual thermoregulation appears to be more important to survival of the pups. In this species, chemical thermoregulation depending on consumption of O_2 and body temperature changes under various ambient temperatures, is well-pronounced only under conditions of higher environmental temperature (28°C-35°C). Thermoregulation appears on day 10 and is completely functional at the end of the third week (BASHENINA, 1960). The results in this study show that thermoregulation is not efficiency before at last 14 days, and certainly not before the pup has reached a minimum body weight which is higher as the temperature is lower.

At 33°C (the temperature at which the pups are smallest) thermoregulation does not seem imperative to survival after weaning. 33°C represents the thermal neutrality point in adult field-voles (RIGAUDIÈRE, 1966).

Partial mortality of some litters may be explained by heterogeneity within the litter. In *Clethrionomys rutilus* the temperature of some individuals in the same litter is regulated at 13-14 days ; others are incapable of this regulation before 17 or 18 days (MORRISON *et al.*, 1954).

The role of the nest in litter thermoregulation is also very important ; it has been noted that survival at 5°C is improved when abundant nest construction material is provided. COTTON and GRIFFITHS (1967) observed that the temperature inside the nest of *Clethrionomys glareolus* does not go lower than 10°C when the outside temperature falls from 15°C to 0°C. In another field-vole, *Microtus ochrogaster*, the pups cannot survive without a nest at temperatures lower than 10°C (GIER and COOKSEY, 1967).

As the temperature rises, the necessity for a nest decreases ; at 33°C pups can live without a nest. In mouse, the mother even disperses the pups when the temperature rises above 32°C (PENNYCUIK, 1964).

In this experiment females were not acclimatized to the experimental temperatures of 5°C and 33°C before parturition. Their feeding and maternal behavior may be modified during the adaptation period, *i.e.* during the suckling period. Food intake in field-vole (CAILLOL and MARTINET, 1976) or in rat (ROUBICEK *et al.*, 1968) and mouse (BARNETT and LITTLE, 1965) decreases when the temperature rises. The mammary gland secretory tissue in mouse is less developed at 34°C than at 21°C (PENNYCUIK, 1966). This may explain that in vole as in rat (HEARNSHAW and WODZICKATOMASZEWSKA, 1973) there is high pup mortality in the first week of lactation and the surviving pups grow slowly when it is hot.

The cold, on the other hand, does not change feeding or maternal behavior. The nest is even better built than at 21°C and the pups are at least as big. However, the pups may not react as well, thus also accounting for mortality after weaning. GEBCZYNSKI (1969) observed that when it was cold the pups did not try to leave the nest and ate rarely. This is also a sign of deficient thermoregulation, at least in hibernating mammals.

The quality of vegetation eaten by the mother, then by the pups, also affects survival rate. The unfavorable role of alfalfa harvested in the fall at a late vegetative stage, has already been noted in a previous study (MARTINET and MEUNIER, 1969). The feeding value of alfalfa probably has direct influence on the mother's milk production and on the young; growth is more or less retarded and we know that weight of the young at weaning is the most important criterium for future survival. Ambient humidity recorded throughout the experiment was not controlled ; so it is not possible to estimate its effect on pup survival and its interaction with temperatures. However it appeared that the hygroscopic properties of the nesting materials protected the interior from excessive moisture or dryness (STARK, 1963). GETZ (1963) did not found any significant difference in the total evaporative water losses of the meadow vole between relative humidity of 50 p. 100 and 96 p. 100 at 27°C. In our study, humidity lower thant 50 p. 100 at 33°C may explain slow body growth as it was shown in the mice (ELLENDORF *and al.*, 1970).

Microtus arvalis, and particularly the pups, are never subjected to a 33°C temperature in the fields. On the other hand, 5°C and 21°C are the mean temperatures at a depth of 20-30 cm in the ground from December to February and in July and August in the Poitou district (table 6). In this district survival rates in the pups during the first month are about 6 to 25 p. 100 from January to April and 30 to 50 p. 100 from July to October (MARTINET and SPITZ, 1971).

TABLE 6

Temperature in the ground at 9 A.M.

Monthly mean from 1967 to 1973 as recorded at Lusignan in Poitou by the forage plant improvement station of the I.N.R.A.

Month	20 cm depth	30 cm depth
December	5.3 ± 0.2	6.0 ± 0.2
January	4.7 ± 0.2	5.3 ± 0.2
February	5.2 ± 0.4	5.7 ± 0.3
July	20.3 ± 0.4	19.9 ± 0.3
August	19.9 ± 0.4	19.9 ± 0.4

The effect of cold temperature and poor food value of alfalfa in the fall on the survival of the young observed in this study may partly explain the figures obtained in nature.

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RÉSUMÉ

INFLUENCE DE LA TEMPÉRATURE SUR LA SURVIE AU COURS DU PREMIER MOIS DE LA VIE CHEZ LE CAMPAGNOL DES CHAMPS, *MICROTUS ARVALIS*, ÉLEVÉ SOUS DIFFÉRENTES CONDITIONS DE PHOTOPÉRIODE ET D'ALIMENTATION

La température d'élevage joue un rôle primordial dans la survie des jeunes campagnols au cours du premier mois de la vie ; plus la température est basse et plus la mortalité augmente. L'absence d'une thermorégulation efficace au moment du sevrage explique cette mortalité

La qualité de la luzerne consommée intervient aussi sur la survie : une luzerne récoltée au printemps à un stade végétatif précoce permet une meilleure survie des jeunes qu'une luzerne récoltée en automne à un stade végétatif plus tardif.

La durée d'éclairement quotien n'intervient pas dans la survie du campagnol de la naissance à un mois.

Les deux facteurs défavorables à la survie, température basse et luzerne d'automne, peuvent expliquer en partie les taux de mortalité observés dans la nature au cours du premier mois de la vie.

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