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eine völlig andere Situation angesehen werden, die die Fledermäuse befähigt, Form und Gestalt der Uferbegrenzung genau zu erkennen, was von lebenswichtiger Bedeutung sein kann. Doch all dies schließt nicht aus, daß Tiere, die z. B. in ein Becken mit glattem Rand geraten, auch ertrinken können, wenn sie aus irgendeinem Grund keine Möglichkeit zum Auffliegen haben.

Zusammenfassung

Beim Schwimmen erweisen sich die beiden Flügel als ausgezeichnete Ruderorgane, die gleichzeitig und gleichsinnig betätigt werden. Der Körper der Fledermäuse bildet mit der Wasseroberfläche einen Winkel von 15 bis 40°, wird mit jedem Flügelschlag auf- und abbewegt und erweckt dadurch den Eindruck des Hüpfens auf dem Wasser. Das Uropatagium wird in geradliniger Fortsetzung des Körpers unter Wasser gehalten.

Von den 5 Phasen der Schwimmbewegung bringen nur 3 positive Effekte. Die Geschwindigkeit des Schwimmens nimmt mit der Größe der Tiere zu, die Zahl der Flügelschläge pro Meter dagegen ab. Bei Richtungsänderungen hält ein Flügel, dem Grad der Änderung entsprechend, mehr oder weniger lange still.

Das Starten vom Wasser ist meist sehr anstrengend, weshalb bis zu 6 Flügelschläge nötig sein können. Geschwächte, ermüdete oder Jungtiere vermögen nicht vom Wasser aufzufliegen. Das Schwimmen bzw. Auffliegen vom Wasser dient primär der Rettung des Lebens.

Die Orientierung während des Schwimmens erfolgt optisch und akustisch. Ultraschallaute werden fast regelmäßig in der 5. Phase der Schwimmbewegungen abgegeben. Die Änderung der Ultraschalllaute in bezug auf ihre Länge, Zahl und Frequenz ermöglicht den Fledermäusen, Form und Gestalt des Ufers genau zu erkennen.

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Anschrift des Verfassers: Prof. Dr. Anton Kolb, Lehrstuhl für Biologie, Universität Bamberg, An der Universität 2, D-8600 Bamberg

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Studying bat echolocation signals using ultrasonic detectors

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Receipt of Ms. 25. 2. 1983

Abstract

Animal ultrasounds can be studied by using detectors that translate these sounds to sonic frequencies. The superheterodyne system produces an audible beat note in proportion to a tuned frequency. The divide-by-ten system produces an output in which the fundamental frequency is lowered by a factor of 10. Here we give an improved design of the divide-by-ten system and compare it to the superheterodyne system during field use. Using detectors has extended our knowledge of the acoustic behavior of bats in the field. Some examples are given. Of special interest is the use of social ultrasound by bats on-the-wing.

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Introduction

Man is no longer limited by his senses when studying natural phenomena. For example, we can "hear" ultrasound (frequencies above 20 kHz) by using special electronic detectors. Many terrestrial animals, especially rodents and bats, use ultrasound for orientation and communication (Sales and Pye 1974). Bats can orient, detect, and catch prey in total darkness using only the echoes of their ultrasonic cries (Griffin 1958; Schnitzler 1978). Here we will describe two relatively inexpensive ultrasonic detectors that can be used for studying bat acoustic behavior, especially in the field.

Insectivorous bats continuously emit ultrasonic cries while flying. The cries are from a few ms up to several tens of ms long. Bats use frequency modulated (FM) sounds as well as constant frequencies (CF) depending on the species and situation. The cries can contain more than one harmonic. Sequences of bat cries can be divided into three portions (Fig. 1).

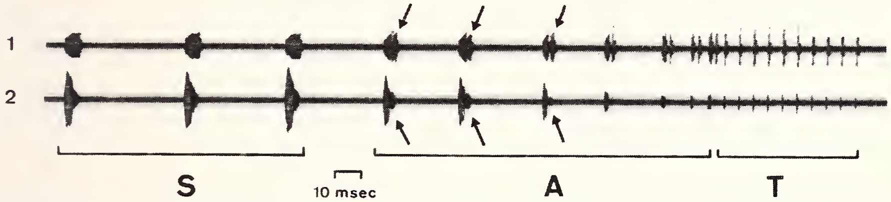

Fig. 1. Bat cries recorded simultaneously using a divide-by-ten detector (trace 1) and a high speed tape recording system (trace 2). Trace 2 shows the amplitude structure of a series of cries from *P. pipistrellus* during insect catching recorded indoors. *S* shows cries from the search phase, *A* shows cries from the approach phase and *T* shows cries in the terminal buzz emitted just prior to capture. The arrows indicate echoes. Note that the detector signal has a constant amplitude

Searching or cruising cries have the longest durations and lowest repetition rates (S in Fig. 1). When a bat detects an insect, the cries become shorter and are emitted at a higher repetition rate. We call this the approach phase (A in Fig. 1). The third phase is the terminal "buzz", which the bat emits just prior to capturing the prey. The terminal buzz contains the shortest cries (as short as 500 µs in some species) coming at the highest repetition rates (as high as 200 per s) (T in Fig. 1). (For a recent review of bat echolocation see Busnell and Fish 1980.)

Field studies are crucial to our understanding of bat echolocation. Our knowledge about the acoustic behavior of bats in the field is limited, but interest in field studies is increasing (Simmons et al. 1979a; Ahlen 1981; Miller and Degn 1981).

The acoustic signals of bats are best studied using a high speed magnetic tape recorder, precision microphones and a computer for analyzing the recordings. Needless to say, such equipment is expensive. The tape recorder can be bulky and sometimes inconvenient to use in the field. Ultrasonic detectors are much cheaper and they can provide general information about acoustic behavior, especially species differences and acoustic behavior in relation to the environment.

Apparatus

Two types of ultrasonic detectors are available. One employs a superheterodyne system while the other divides the incoming signal by ten, a so-called divide-by-ten detector. The superheterodyne system employs a tunable filter and a series of fixed (comb) filters covering the frequency range used by most bats (10 kHz to 180 kHz). When the device is tuned near to a frequency in the bat's cry an audible beat note is generated. A

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superheterodyne ultrasonic detector is commercially available from QMC Instruments Ltd., 229 Mile End Road, London El 4AA, England.

The divide-by-ten detector was first developed by us (see ANDERSEN and MILLER 1977). The device produces one cycle at the output for every ten cycles at the input for frequencies from 15 kHz to 150 kHz. The output (1.5 kHz to 15 kHz) can be heard and recorded on conventional tape recorders. Since the microphone is designed for audible frequencies we use an adjustable "digital" filter to set the lower frequency limit at 15 kHz. The upper frequency limit is determined by the sensitivity of the microphone. The frequency/time structure of the original signal (cry) is translated rather accurately by the detector (Fig. 2).

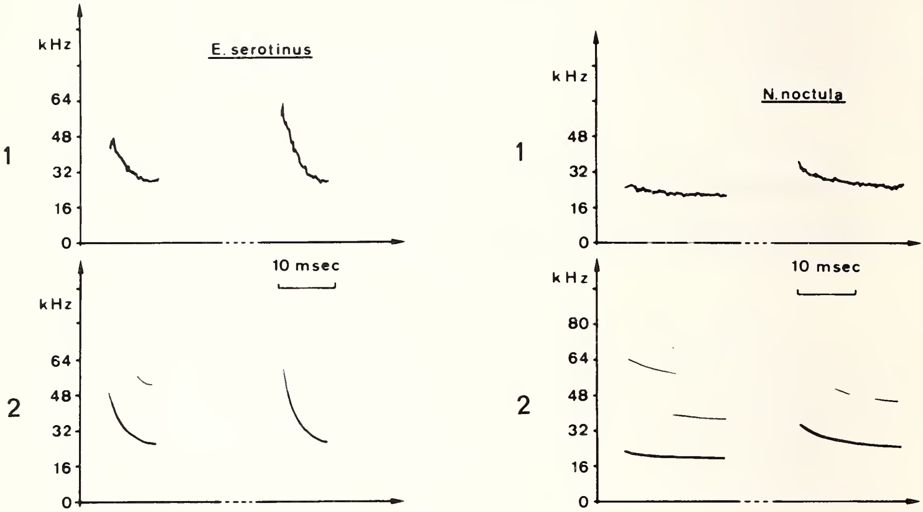

Fig. 2. Frequency structure of bat cries recorded in the field. Spectrographs (2) show harmonics in some cries. Note that the detector signals as analyzed with a period meter (1) show only the first harmonic. (From MILLER and DEGN 1981, with permission)

Trace 2 shows spectrographs of cries from *Eptesicus serotinus* and *Nyctalus noctula.* Trace 1 shows the same cries recorded (simultaneously) via the detector and analyzed for frequency content (using a period meter). Only the most intense frequency components are divided (here the first harmonic). The instruments faithfully reproduces cry durations and repetition rates. This is shown in Fig. 1 where recordings from a pipistrelle bat *(Pipistrellus pipistrellus)* were made simultaneously using a divide-by-ten detector (trace 1) and a high speed tape recording system. Information regarding sound intensity is lost (compare traces 1 and 2 in Fig. 1).

An up-to-date circuit diagram is shown in Fig. 3 and a component list is given in the Table. We use inexpensive electret transducers as microphones. The microphone amplifier (IC_1 in Fig. 3) should be assembled in the microphone holder. The microphone should be mounted on a thin holder to minimize disturbance of the sound field. The overall sensitivity of the detector (using the CA 2889 electret microphone) is typically about 54 dB sound pressure level (SPL) (20 kHz to 60 kHz) and about 70 dB SPL (70 kHz to 120 kHz) when the sensitivity is set just above the noise level. (SPL is referred to 20 μPa, which is about the threshold of human hearing at 2 kHz.) The transducer can be made 4 to 6 dB more sensitive (50 to 140 kHz) by removing the protective disk covering the membrane of the electret microphone. By throwing a switch one can record voice notes (IC_{1c} in Fig. 3). A divide-by-ten detector is commercially available from WESTEC Services, Inc., 3211 Fifth Avenue, San Diego, California, 92103, USA.

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The simplest way to analyze recordings made with a divide-by-ten detector is to use an oscilloscope and measure relevant parameters directly. However, we use a computer to analyze recordings. The program produces a plot similar to a histogram where the ordinate of each dot represents the reciprocal of the time interval between two consecutive cycles of the (divided) cry (Fig. 5). A number above a cry indicates the duration in ms and a number below and between two cries indicates the interval between the cries in ms. The program "condenses" information by not using a time axis. (The cry is slightly distorted in the process.) We have also used a period meter to analyze cries (Fig. 2 trace 1). A circuit diagram for a period meter and a review of apparatus for studying animal ultrasound can be found in SIMMONS et al. (1979b).

Use of ultrasonic detectors

Recordings via ultrasonic detectors cannot substitute for actual recordings of animal ultrasounds. Nevertheless, useful information can be obtained, but one must be aware of certain limitations. These can be illustrated by considering each parameter of the bat's signal.

Cry repetition rates are reproduced by both types of detectors.

The maximum error in the duration of a cry is 9 cycles for the divide-by-ten detector. This error is maximum at 15 kHz,

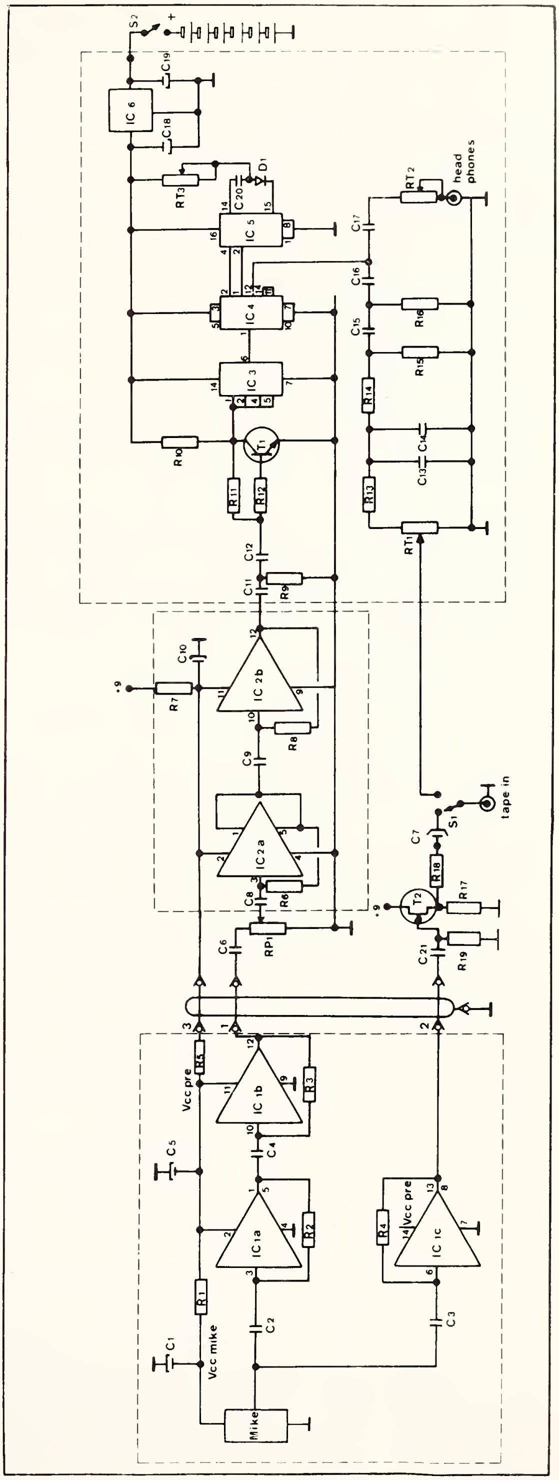

Fig. 3. Circuit diagram of a divide-by-ten detector. The components are given in the table

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Table

Component list

Resistors						Capacitors		
R1	1.8 K	1/8 W	RP_1	47 K	1/4 W	C1+5	2.2 MF	tental
R2+3	100 K	1/8 W				C2+4+8+9	1 nF	
R4	1 M	1/8 W	RT_1	10 K	1/4 W	C3	1.5 MF	tental
R5	1.5 K	1/8 W	RT_2	10 K	1/4 W			
R6+8	100 K	1/4 W	RT_3	100 K	1/4 W	C6	680 pF	
R7	1.8 K	1/4 W				C7	1.5 MF	
R9+12+14	22 K	1/4 W				C10	33 MF	
R10	10 K	1/4 W				C11+14	220 pF	
R11+13	120 K	1/4 W				C12	2.2 nf	
R15	2.2 K	1/4 W				C13	1 nf	
R16	220 ohm	1/4 W				C15+17	68 nf	
R17	4.7 K					C16	680 nf	
R18	470					C18+19	3.3 MF	
R19	1 M					C21	1 n	
						C20	4.7 n	

Diodes	
D1	IN 4001

Transistors	
T1	BC108c
T2	2N4302

Integrated circuits		
IC 1	a-b-c	CA3600E
IC 2	a-b	CA3600E
IC 3		SN74LS13
IC 4		SN74LS90
IC 5		SN74LS123
IC 6		LM78L05

Microphone
CA 2889, Knowles Electronics Ltd., Victoria Road, Burgess Hill, RH15 9LP, Sussex, England.

superheterodyne detector, the situation is somewhat more complicated. The instrument must be tuned to the center frequency of the cry. For an FM signal the change of frequency must fall within the band width of the built in filter. Fig. 4 shows simultaneous recordings from a divide-by-ten detector (trace 2) and a superheterodyne instrument (trace 1) made on a stereo cassette tape recorder. In Fig. 4A (*E. serotinus* cry) the durations are comparable for a cry with a slow frequenc sweep. But in Fig. 4B (*Myotis daubentoni* cry) the duration is much shorter when recorded with the superheterodyne detector. This may be due to the rapid frequency sweep typical of this species.

The divide-by-ten detector accurately translates the frequency/time structure of the most intense components of the original cry (Figs. $2A_1$, $2B_1$, $4A_2$ and $4B_2$). The signals must be recorded for later analysis. One can determine the frequency structure fairly accurately with the superheterodyne detector, provided that the instrument is not overloaded by intense cries. Frequency determinations must be done during observations when using a superheterodyne detector, since recordings contain no frequency information that can be related to the cry (Fig. $4A_1$ and $4B_1$).

Information on intensity is lost in the divide-by-ten detector (see Fig. 1). The superheterodyne detector retains information on relative intensities. However, accurate measurements of sound intensity are difficult in the field. Microphone directionality, the directionality of the bat's sound emission, and the attenuation of ultrasound in air all contribute to the problem. Even the relative intensities of harmonics in a single cry are

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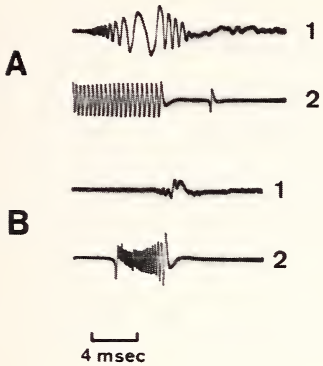

Fig. 4. Simultaneous recordings of bat cries using a superheterodyne detector (trace 1) and a divide-by-ten detector (trace 2). *A* shows a cry from *E. serotinus* and *B* shows a cry from *M. daubentoni.* Note that the superheterodyne signal contains no frequency information related to the actual cry. Cry durations are comparable in *A* but not in *B* (see text)

distorted unless the microphone and holder are small with respect to the wavelength of sound. This is usually not the case. All of these factors make it difficult to interpret intensity information.

The distance at which a bat can be detected is a function of the intensity of the cry and the sensitivity of the detector. The noctule bat *(N. noctula)* can be detected at about 30 m using the divide-by-ten detector, and at about 100 m when using a superheterodyne detector with narrow band tuning. The superheterodyne detector is about 20 to 30 dB more sensitive than the divide-by-ten detector, owing to the tunable filter system.

Observations

Since ultrasonic detectors are light weight, their widest application is in field studies of animal ultrasound. We have used them mostly to study the acoustic behavior of bats, but insect and rodent ultrasounds can also be studied.

Probably the most surprising result of our field studies (and those of others) in that certain species of bats are much more flexible in their acoustic behavior than anticipated from laboratory studies (Sales and Pye 1974; Simmons et al. 1979a; Miller and Degn 1981). Some of this flexibility can be correlated with the bat's acoustic environment. For example, the bat *P. pipistrellus* uses only FM cries when flying indoors. (The cries shown in Fig. 1 are FM.) But, in the field these bats can use FM/CF cries (Fig. 5A). Presumably, the CF portion of the cry assists the bat in detecting echoes from distant or moving (?) targets in the field. Bats of this species can even change the frequency of the CF portion when they are flying in groups (compare the two 8 ms cries in Fig. 5A). Perhaps they do this to avoid interference from a neighboring bat. The pipistrelle bat drops the CF portion when pursuing prey (Fig. 5B).

A number of species will use social vocalizations while flying in the field. *P. pipistrellus* emits ultrasonic vocalizations when one bat chases another (Fig. 5A, the star). The frequency band of social vocalizations lies below that used for echolocation in pipistrelle bats.

Bats can be identified solely on the basis of their cries after one knows the species and its acoustic behavior (compare the cries presented in Figs. 2 and 5). However, identification in the field tends to be subjective; based on qualities of the auditory signal as translated by the detector. This is especially true when bats cannot be seen. As a result, one must know the acoustic behavior of each species in some detail before positive identification can be made. Once the acoustic behavior has been correlated with the species, identification via the detector signal alone is possible. (This is true at least of the divide-by-ten detector.) There are some closely related species, however, that are extremely difficult to identify acousti-

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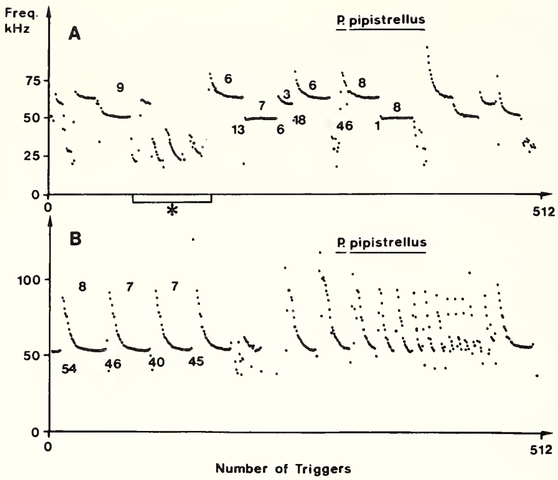

Fig. 5. A computer analysis of bat cries recorded in the field using a divide-by-ten detector. *A* shows a recording from a group of pipistrelle bats *(P. pipistrellus).* Note the pronounced use of CF components. Pipistrelle bats will also emit social ultrasounds while foraging in the field (the star). *B* shows a recording from a single pipistrelle bat during pursuit and capture of prey. Note how the CF component is eliminated during the approach and terminal phases. Numbers above cries indicate cry durations in ms while numbers below indicate cry intervals in ms. See text for more details

cally, for example *Myotis daubentoni* and *M. dasycneme.* At present we know rather little about the acoustic behavior of *M. dasycneme.*

Some animal ultrasounds are difficult or impossible to detect using ultrasonic detectors. Certain butterflies can produce intense impulse-like ultrasounds that presumably function as bat-repellent signals (Møhl and Miller 1976). These sounds are composed of less than 10 cycles and thus cannot be detected on a divide-by-ten detector. Such sounds could easily be missed by a superheterodyne detector owing to problems in tuning.

In conclusion, ultrasonic detectors can be useful for studying animal ultrasound. Interpretations, however, must not extend beyond the limits of the instrument used.

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Zusammenfassung

Ultraschall-Meßgeräte für Echoortungslaute von Fledermäusen

Ultraschall-Tierlaute können mit Detektoren untersucht werden, die Ultraschall in Schall übersetzen. Überlagerungsdetektoren erzeugen hörbaren Schall mit einer Frequenz proportional zur Einstellfrequenz. Zehntelfrequenzsysteme ergeben ein Zehntel der Ultraschallfrequenz. In dieser Arbeit wird die verbesserte Konstruktion eines Zehntelfrequenzsystems beschrieben und im Freilandversuch mit dem Überlagerungsdetektor verglichen. Diese Meßgeräte haben unser Wissen über das akustische Verhalten von Fledermäusen erweitert. Einige Beispiele werden beschrieben. Besonders interessant sind soziale akustische Signale von fliegenden Fledermäusen.

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The den system of the Alpine marmot *(Marmota marmota marmota)* in the National Park of Stelvio, Northern Italy

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Museo Civico di Storia Naturale, Milano, Italia

Receipt of Ms. 21. 3. 1983

Abstract

Studied the den system of the Alpine marmot which consisted of a variable number of chambers, the principal one being lined with thick litter, with openings and tunnels that linked them with the outer surroundings.

Openings were divided into four types which differed in their use and location within the animal's home range.

A qualitative and quantitative analysis of the den system showed a positive correlation between the slope and the opening's orientation; the gradient of the first 30 cm of the tunnel differed between the principal and secondary openings.

Exposure to wind was suggested as the main factor affecting the non-random arrangement of the openings.

Introduction

The behavioural and ecological characteristics in the genus *Marmota* have been studied in detail by Armitage (1962, 1965, 1973, 1974, 1975, 1977, 1979), Downhower and Armitage (1971), Barash (1973a, 1973b, 1974a), Svendsen (1974). The American researchers by analysing their six Nearctic species obtained a clear picture of the relationships between environment and social structure, and outlined a hypothesis on the evolution of society in the genus *Marmota* (Barash 1974b) later criticized by Andersen et al. (1976).

In this connection, however, it is surprising the meagre attention paid to some interesting papers on the ecology and psychology of the Alpine marmot previously published (Bopp 1954, 1955, 1956, 1966; Müller-Using 1954, 1956, 1957; Psenner 1956, 1957, 1960; Münch 1958; Couturier 1964; Zelenka 1965). According to Armitage and Downhower (1974) the quality of hibernacula (places in which marmots spend the winter) and the quantity of fat accumulated before winter may influence the survival of the young yellow-bellied marmots *(Marmota flaviventris)* through hibernation.

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