AUTUMN POPULATION DENSITY OF THE EDIBLE DORMOUSE (GLIS GLIS) IN THE MIXED MONTANE FOREST OF CENTRAL SLOVENIA OVER 33 YEARS

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Data were obtained during traditional autumn trapping of the Edible dormouse *Glis glis* in the mixed montane forests of central Slovenia, between 1968 and 2000. Altogether 2235 dormice were trapped in 4335 trap nights. Fifteen years were of low population density, three years were of medium density and fifteen years were of high density. The mean duration of a low density phase was 1.50±0.707 years (range 1–3; N = 10) and of a high density was 1.25±0.452 years (range 1–2; N = 12). The mean interval between low densities was 1.56±1.014 years (range 1–4; N = 9) and between high densities was 1.55±0.820 years (range 1–3; N = 11). Thus, on average, approximately 1.5 years of high density were followed by a similar period of low density, a pattern roughly suggesting three years cyclicity. Juveniles strongly predominated in high density years, but not in low density ones. Autoregressive moving average model (ARIMA) time series analysis of population densities did not uncover any pattern, consequently the resulting model had no predictive power.

Key words: *Glis glis*, population densities, time series analysis

INTRODUCTION

It is well-known that small rodent populations are prone to pronounced oscillations over the years, the causes and regulation of which are still disputed (HANSKI & HENTTONEN 1996, FELDHAMER *et al.* 1999). Such oscillations have been widely studied in murids amongst which lemmings and some voles (particularly *Microtus* and *Clethrionomys* species) tend towards clear periodicity in their peak densities with cycles of 3 to 4 years (STENSETH & IMS 1993). Regular oscillations are characteristic of short-lived small rodents that are markedly r-selected and occur in structurally simple boreal or grassland ecosystems (FELDHAMER *et al.* 1999). Dormice (Gliridae), on the other hand, generally tend to be rare in small mammal assemblages, live at low population densities and have a relatively low reproduction rate. According to rodent standards they are best described as K-selected.

The Edible dormouse *Glis glis* (LINNAEUS, 1766) is the largest species of the dormouse family (Gliridae), whose range mainly coincides with the deciduous for-

ests of Europe and adjacent regions of the Near East. It is rare in many parts of its area and particularly in the north it is of conservation concern (MITCHELL-JONES *et al.* 1999). On the other hand, it is usually common in southern Europe, where it has been exploited as a commodity species for centuries, if not millennia (CARPA-NETO & CRISTALDI 1994). It has also been known for a long time that population densities fluctuate widely, and in consequence so does trapping success (DESCH-MANN 1883). The amplitude of cyclic abundance is so enormous, at least in some parts of the Edible dormouse's range, that in the past people have believed that overabundant autumn densities were due to the impact of supra-natural forces (Fig. 1). Hardly any scientific attention has been paid to these fluctuations and the population biology of the Edible dormouse at various population densities remains largely unknown. The basic problem is lack of a long-term monitoring of any Edible dormouse population, accompanied by detailed information on demographic parameters.

Fig. 1 Enormous oscillations in autumn densities of the Edible dormouse, which has been regarded as a commodity species in Slovenia since at least 1240, justified a belief that the devil is their shepherd. Reproduced from VALVASOR (1689)

However, several studies of short to medium duration are available. For Baden-Württemberg (Germany) KULZER *et al*. (1993) and SCHLUND and SCHARFE (1997) reported density changes (as percentage of occupied nest boxes) between 1979 and 1994. They recorded six peaks with five intervening lower density years. There was a clear trend over the entire study towards a gradual increase in percentage of nest boxes occupied. The periodicity was 2–3 years (mean = 2.33 years, N = 6) and the largest amplitude was *c*. 15-fold. LOZAN *et al.* (1990) found a very different pattern in Moldavia between 1967 and 1979, with a periodicity of eleven years and an amplitude of *c*. 15-fold. The pattern detected by VIETINGHOFF-RIESCH (1955) between 1949 and 1954 in Niedersachsen, Germany, was also unique. A pronounced peak in 1949 was followed by a crash in 1950 (amplitude of 11.3-fold), and by a subsequent three years (1951–1953) of moderate density; 1954 was again a low density year. In high/moderate density years, the number of juveniles exceeded the number of adults while the opposite was the case in the two low density years (VIETINGHOFF-RIESCH 1955).

In the study by SCHLUND & SCHARFE (1997), peak years coincided with mast years of beech and oak, the two key trees in the Holarctic deciduous forest ecosystem (SORK *et al*. 1993). These trees are mast seeders, producing large seed crops every two to six years, while production in the intervening years is low or even fails (RÖHRIG & ULRICH 1991). Since reproduction in the Edible dormouse evidently depends on mast seed availability (VIETINGHOFF-RIESCH 1955, BIEBER 1998), peaks in density are likely to reflect simple increase in the reproductive rate of the same year.

In the present paper we analyse data obtained by traditional dormouse hunting, which permit an insight into population dynamics and age structure over 33 years. To the best of our knowledge, no other time series of comparable length has been published for the edible dormouse.

MATERIAL AND METHODS

Field work was carried out in the extreme north-western part of the Dinaric Alps, west of the town of Vrhnika (central Slovenia; altitude 293 m above sea level). This is a mountainous region (elevation ca. 500 m) densely covered by beech (*Fagus sylvatica)* and fir (*Abies alba)* forests on corroded limestone bedrock. The climate is humid continental, with warm summers (mean July temperature in Vrhnika is 19.2 °C) and cool winters (mean January temperature is 1.4 °C). Annual mean temperature is 9.3 °C and 91.7 days on average have mean temperatures below freezing point. Annual precipitation amounts to 1600 mm, with 150 days receiving >1 mm of rainfall.

The basic source of information was the field records kept by a traditional dormouse hunter (see PERŠIČ 1998, and references therein for details on the tradition of dormouse hunting in Slovenia). This particular hunter trapped dormice using native snap traps, set on trees (mainly > 3 m above

grounds) in places where a catch was likely to occur. Thus, we believe that the methodology was consistent enough to detect crude pattern in density fluctuations over the years. In accordance with tradition and legislative requirements (which allow dormouse hunting from September 25 to November 15), trapping was performed in September and October. Between 8 and 29 traps were used in a single night (mean = 18.8±3.99, N = 236 nights). Trapping intensity depended on the bag, time when dormice enter hibernation, and time restrictions posed by the personal obligations of the hunter. In low density years trapping intensity and success were also low. Consequently, traditional hunters carefully monitor beech masting and dormouse activity in the spring and summer, trying to predict the harvest in the forthcoming autumn. The hunter kept records on the number of traps set each night and number of dormice caught, mainly according to age. Juveniles were defined as animals of the same year while adults are those which had hibernated at least once. Such distinction is possible on the basis of general appearance of Edible dormice (body proportions, fur coloration) and body mass.

Trapping effort varied significantly between years. We standardise this by calculating number of dormice caught per 100 trap nights (TN).

To uncover possible hidden patterns in the data, and to generate predictions, we applied autoregressive moving average model (ARIMA) time series analysis. Initial data were transformed to natural logarithms in order to stabilise the variance. The parameters of the analysis were estimated in such a way as to minimise the sum of squared residuals. An autocorrelation is the correlation of a series with itself, shifted by a particular lag. In our case, the correlogram presents these autocorrelations for lags from 1 to 15. (See Statistica user manual (1995) for more methodological details and FRAMSTAD et al. (1993) for application in analysing animal population fluctuations). Statistical tests were run in Statistica (Release 5.5, 1999).

RESULTS AND DISCUSSION

Trapping results – Altogether 2235 edible dormice were trapped in 4335 trap nights. Trapping was carried out in 24 seasons out of a possible total of 33 (Table 1). For the remaining nine years (1969, 1976, 1978, 1979, 1981, 1983, 1985, 1987, 1996) the autumn densities were estimated to be too low for trapping to be worthwhile or no dormice at all were confirmed during night surveys. All these years were considered as having densities equal to zero. During the remaining 24 years, the dormice were trapped on between one and 23 nights and the total number of TN per season varied from 10 to 438.

Trapping effort (expressed as the number of TN within a season) depended heavily on the density of a population (i.e. number of dormice per 100 TN); the fit was positive and highly significant (r = 0.787, $p < 0.00001$; Fig. 2). This is possibly one source of error since low density years remained undersampled. However, trapping intensity (TN per season and TN per night) did not remain the same over the entire period even in peaks years (Fig. 3). The depression in the first half of the 1970s was partly due to adverse weather conditions (rainy nights), but also to some private engagements of the trapper. A sharp decline in the trapping effort during the 1990s was most likely due to the advanced age of the trapper. In general, trap-
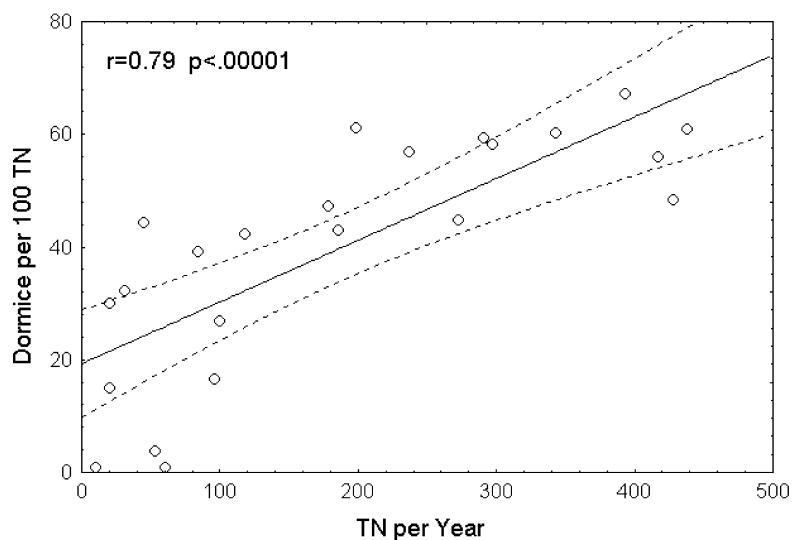
Fig. 2 Plot of dormouse density (dormice per 100 trap nights (TN)) against the number of TN per year, with 95% confidence limits given for the regression line

Table 1. Results of trapping Edible dormice by month and year. Relative population density: H = high, M = medium, L = low

Year	Density	TN	Dormice	Year	Density	TN	Dormice
1968	H	417	234	1985	L	0	0
1969	L	0	0	1986	H	393	264
1970	H	237	135	1987	L	0	0
1971	H	178	84	1988	L	20	0
1972	M	100	27	1989	H	438	267
1973	H	343	207	1990	L	10	0
1974	L	60	0	1991	H	297	173
1975	L	96	16	1992	H	186	80
1976	L	0	0	1993	L	53	2
1977	H	198	121	1994	H	45	20
1978	L	0	0	1995	H	84	34
1979	L	0	0	1996	L	0	0
1980	H	291	173	1997	L	20	3
1981	L	0	0	1998	M	31	10
1982	H	272	122	1999	H	118	50
1983	L	0	0	2000	M	20	6
1984	H	428	207				

Table 2. Variation in the percentage of juvenile Edible dormice according to month in various years. Total number of dormice collected is in parentheses. Significance levels (χ^2 test: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ns: not significant at $p < 0.05$. Last day of October when adults/juveniles were collected (only years with an adequate density of sampling days were considered)

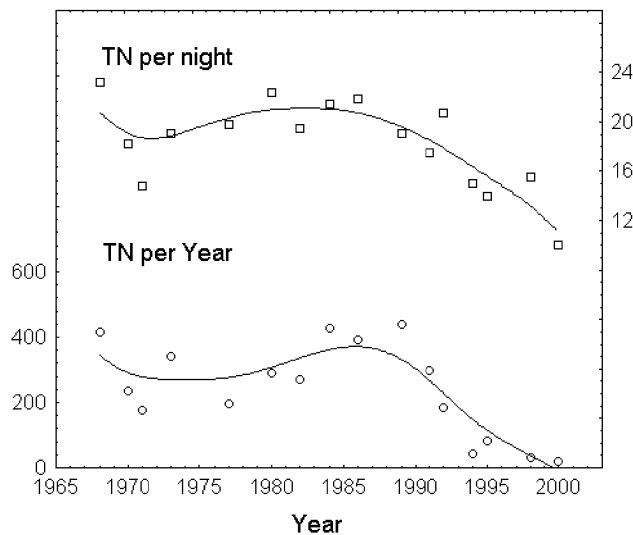| Year		September	October	Last day
1970**	H	64.0 (25)	89.6 (96)	8/15
1971	H		92.6 (84)	9/15
1972*	M	60.0 (10)	94.1 (17)	3/4
1973***	H	69.4 (49)	91.2 (137)	8/12
1975	L	46.2 (13)		
1977*	H	77.6 (49)	94.6 (56)	7/11
1980	H		91.1 (169)	6/20
1982ns	H	91.7 (12)	90.0 (110)	14/21
1984****	H	31.7 (63)	91.0 (144)	17/26
1986****	H	64.2 (53)	91.5 (211)	16/18
1989**	H	83.4 (44)	95.5 (223)	14/24
1991***	H	83.1 (71)	97.4 (114)	4/15
1992*	H	78.8 (47)	96.4 (28)	
1993	L	33.3 (3)		
1999ns	H	100 (8)	90.2 (41)	
2000	M		80.0 (5)	

Fig. 3. Variation in number of trap nights per year and per night, respectively, between 1968 and 2000. Only high density years are included. The lines are the least square fit. See text for further explanation

ping effort was more intense in October (with 72.2% of all TNs and 70.7% of all trapping nights) than in September, which may reflect regional traditions in dormouse trapping.

Density fluctuations – We divided densities into three arbitrary categories: low (<20 dormice per 100 TN), medium (20–40 dormice per 100 TN) and high (>40 dormice per 100 TN). Fifteen years (45.5%) were thus classified as of low density, three years as of medium density (9.0%), and fifteen years as of high density (45.5%; Table 1). Mean duration of a low density phase was 1.50±0.707 years (range 1–3; N = 10) and of a high density phase was 1.25±0.452 years (range 1–2; N = 12). The median was one year in both cases. Similarly, the mean interval between low densities was 1.56±1.014 years (range 1–4; N = 9) and between high densities was 1.55 ± 0.820 years (range 1–3; N=11); again, median was one year in both cases. Thus, on average, approximately 1.5 years of high density were followed by a similar period of low density, a pattern roughly suggesting a three year cyclicity (range of cycles = 2–5 years). In nine cases a high density season followed a low density one and only in three cases was it preceded by a high density year, thus resulting in two consecutive high density seasons.

The amplitude showed much higher variance (coefficient of variation CV≅100%) than the period (CV = 8.9%). Although the value given for amplitude is a crude estimate, due to unreliable density estimates for low density years, the re-
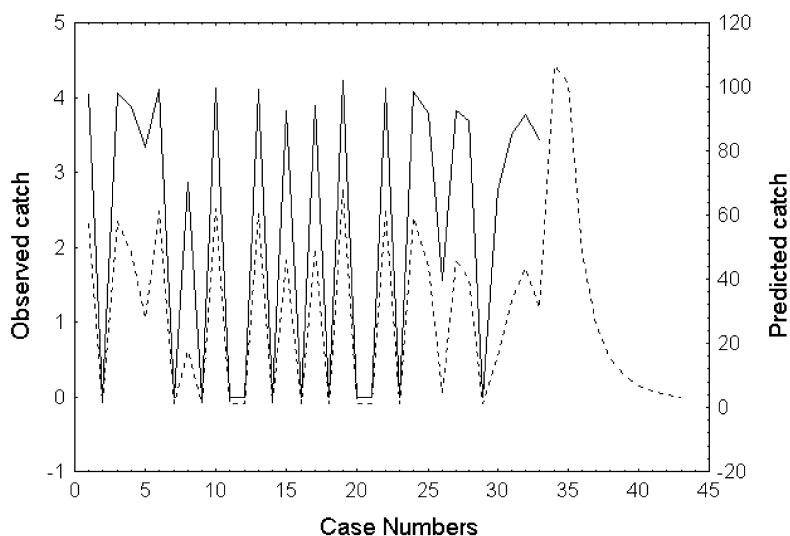

Fig. 4 Observed time series of population fluctuations of Edible dormice in relative numbers transformed to natural logarithms (= catch / 100 TN +1; solid line), with predicted fluctuations from the time series model AR-1 and MA-3 (broken line)

sults agree with the pattern reported for r-selected murids with oscillating populations (STENSETH & IMS 1993).

Age structure – Data on the age structure were available for sixteen years, eleven of which provided information for both September and October. In nine years the share of juveniles was significantly higher in October than in September (Table 2). Coefficient of variation in the percentage of juveniles in a total catch was much higher in September (CV = 24.6%; N = 8) than October (CV = 2.9%; N = 12); only monthly samples with N > 20 were considered. A high incidence of juveniles in October samples is likely for at least two reasons: (i) the adults go into hibernation before the juveniles, and (ii) juveniles from late litters still continue to be recruited into the active population in October. Our data set clearly shows that adults had disappeared from the October samples 1–14 days (mean = 7.00±4.123; N = 11) earlier than juveniles (Table 2) which accords with the first explanation. Besides, the median September adult density was higher (13.1 adult dormice per 100 TN) than for October (3.9 per 100 TN) and the difference was highly significant (Kruskal-Wallis H = 7.435, $p < 0.01$).

The second hypothesis predicts higher juvenile density (i.e. higher number of juvenile dormice per 100 TN) in October than in September. Our data do not support this. Although the median was higher for October (48.8 juveniles per 100 TN)
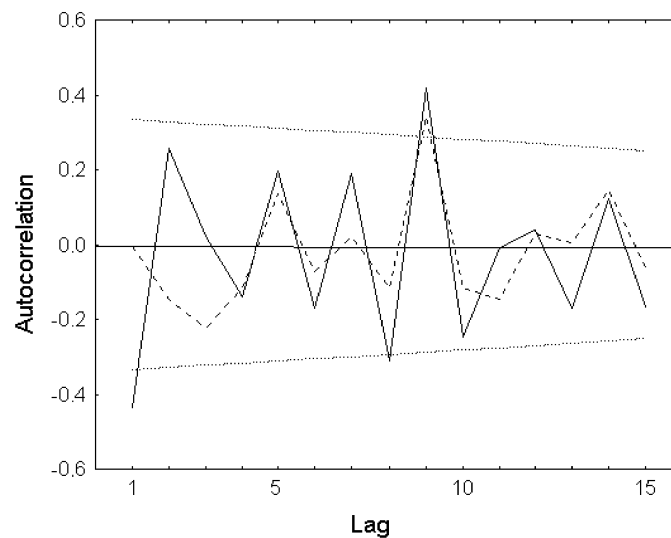

Fig. 5 Correlograms for the autocorrelations of the observed time series of Edible dormice (relative numbers transformed to natural logarithms; solid line) and of the time series of residuals after fitting the predictive model AR-1, MA-3 (broken line). Dotted line indicates confidence limits for ± 2 standard error

than for September (40.7 juveniles per 100 TN), the difference was not significant (Kruskal-Wallis H = 1.812, $p = 0.178$). However, in south-central Slovenia about one-third of the juvenile population attains a body mass >115 g (which is presumed to enable successful hibernation) already by the first ten days of October (authors' unpubl. data). Juveniles from early litters may thus start to leave the trappable population for hibernation already in the first half of October and are subsequently replaced by juveniles from later litters. If so, the actual density of juveniles would be even higher than reflected by trapping results.

Our results are selective, particularly as the majority of samples refer to high density years. From the point of age structure, low density years are badly under represented (two years only) with data being available only for September. However, when dealing with a hibernating rodent like the Edible dormouse, one should keep in mind that trapping can detect only the active portion of the population. In mast years with an abundance of food and consequently high reproductive rate, the share of active animals is presumably higher throughout the year and departure into hibernation is postponed into October. Several short-term field studies indicate that dormice terminate their activity later in reproductive years than in non-reproductive ones (e.g. BIEBER 1998, SVCHLUND & SCHARFE 1997, own unpubl. data). Late autumn sampling is thus likely to indicate the reproductive success but not the adult population density.

Time series analysis – Of several models with various AR and MR terms, the one presented in Figure 4 resulted in the lowest residual mean square error (RMS = 3.855). This model had no predictive power at all since the curve for predicted catch crashed and did not indicate any cyclicity. The correlogram (Fig. 5) suggests periodicity of 2–3 years. Significant or near significant autocorrelations appeared for lags 1, 8, 10 (all negative) and 9 year (positive). Negative autocorrelation with lag of one year could be expected according to the above statement that a peak density year is more likely to follow a low density year than another high density one. More enigmatic are significant autocorrealtions for lags 8–10 which we are unable to interpret. In conclusion, time series analysis did not uncover a regular and predictable pattern in the 33 year sequence of population densities.

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REFERENCES

BIEBER, C. (1998) Population dynamics, sexual activity, and reproductive failure in the fat dormouse (Myoxus glis). *J. Zool., Lond.* **244**: 223–229.

CARPANETO, G. M. & CRISTALDI, M. (1994) Dormice and man: a review of past and present relations. *Hystrix* **6**: 303–330.

DESCHMANN, C. (1883) Der Billichfang in Krain. *Zeitschrift des Deutschen und Oesterreichischen Alpenvereins* **14**: 121–135.

FELDHAMER, G. A., DRICKAMER, L. C., VESSEY, S. H. & MERRITT, J. F. (1999) *Mammalogy. Adaptation, diversity, and ecology*. McGraw-Hill, Boston, 563 pp.

FRAMSTAD, E., STENSETH, N. C. & ŘSTBYE, E. (1993) Time series analysis of population fluctuations of Lemmus lemmus. Pp. 97–115. *In* STENSETH, N. C. & IMS, R. A. (eds) *The biology of lemmings*. Linnean Society Symposium series No. 15, Academic Press, London.

HANSKI, I. & HENTTONEN, H. (1996) Predation on competing rodent species: a simple explanation of complex patterns. *J. Anim. Ecol.* **65**: 220–232.

KULZER, E., LINDEINER-WILDAU, A., VON & WOLTERS, I.-M. (1993) Säugetiere im Naturpark Schönbuch. Übersicht über die Biologie der Arten und Ergebnisse einer faunistisch-ökologischen Untersuchung in den Jahren 1989–1991. *Beih. Veröff. Naturschutz. Landschaftspflege Bad.-Württ.* **71**: 1–212.

LOZAN, M., BELIK, L. & SAMARSKIJ, S. (1990) *Soni (Gliridae) yogo-zapada SSSR*. Molldavskii gosudarstvenii univerzitet im. V. I. Lenina, Kishniev, 189 pp.

MITCHELL-JONES, A. J., AMORI, G., BOGDANOWICZ, W., KRYŠTUFEK, B., REIJNDERS, P. J. H., SPITZENBERGER, F., STUBBE, M., THISSEN, J. B. M., VOHRALIK, V. & ZIMA, J. (1999) *The Atlas of European Mammals*. Poyser Natural History, London, 484 pp.

PERŠIČ, M. (1998) Dormouse hunting as part of Slovene national identity. *Natura Croatica* **7**: 199–211.

RÖHRIG, E. & ULRICH, B. (1991) *Ecosystems of the World 7. Temperate deciduous forests*. Elsevier, Amsterdam, 635 pp.

SCHLUND, W. & SCHARFE, F. (1997) Unterschiede zweier Siebenschläfer-Populationen (Myoxus glis L.) im Schönbuch in Abhängigkeit des Lebensraumes. *Veröff. Naturschutz Landschaftspflege. Bad.-Württ.* **71–72**: 459–484.

SORK, V. L., BRAMBLE, J. & SEXTON, O. (1993) Ecology of mast-fruiting trees in North America. *Ecology* **74**: 528–541.

STATISTICA (1995) Vol. III: *Statistics II*. 2nd ed. StatSoft, Tulsa, OK.

STENSETH, N. C. & IMS, R. A. (1993) Population dynamics of lemmings: temporal and spatial variation – an introduction. Pp. 61–96. *In* STENSETH, N.C. & R.A. IMS (eds) *The biology of lemmings*. Linnean Society Symposium series No. 15, Academic Press, London.

VALVASOR, J. B. (1689) *Die Ehre des Hertzogthums Crain*. Laibach. Reprinted in 1977 by Mladinska knjiga, Ljubljana, 365 pp.

VIETINGHOFF-RIESCH, A., VON (1955) Neue Untersuchungen über die Biologie des Siebenschläfers, *Glis glis glis* (Linne, 1758), auf Grund von Freilandmarkierung im Deister, Niedersachsen, und Beobachtungen im Tierhaus in Hannoversch-Münden. *Säugetierkd. Mitt.* **3**: 113–121.