Inter- and intra-sexual segregation of chamois *(Rupicapra rupicapra)* by altitude and habitat during summer

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Abstract

Studied the late summer distribution patterns of chamois *(Rupicapra rupicapra)* in the Bavarian Alps for purposes of quantitatively describing dispersion and habitat use of female groups, male groups and solitary males and for examining reasons for segregation. Observed groups were classified by group type, elevation and habitat type. Forage plant biomass was determined for the major habitat types by clipping 0.1 m^2 quadrats. Female groups occupied the highest elevations. The mean elevation of occupation was the same for solitary males and male groups but solitary males used a wider range of altitudes. Single males were least selective of habitat type and male groups were most selective. Food quality and quantity was found to be positively correlated with elevation. The hypothesis that males exclude females from better foraging areas is therefore rejected. A model based on conflicting demands for forage and solitude is presented to explain between-population differences in distribution patterns of solitary males. Where food is abundant and population density high, solitary males are predicted to concentrate at lower elevations and not overlap widely with other social classes. Where food is abundant but population density is low, solitary males are predicted to occupy a broad range of altitude zones and overlap extensively with other chamois.

Introduction

One of the most poorly understood aspects of ungulate behaviour concerns why so many social ungulates exhibit marked spatial segregation of the sexes and of male age-classes outside of the rutting season. Many plausible explanations have been advanced for these phenomena (e.g. Geist and Petocz 1977; Geist and Bromley 1978; Clutton-Brock et al. 1982).

Chamois *(Rupicapra rupicapra)* exhibit a complex dispersion pattern with three distinct groups types evident during the summer each occupying separate but overlapping ranges. Female groups, containing adult females, kids, and yearlings, generally occupy higher altitude alpine habitats. Male groups, comprised mainly of young males, occupy mid-elevations both above and below timberline. Lastly, fully mature, prime males remain alone and quite sedentary and occupy a range of elevations from high alpine to low altitude deciduous forests bordering cultivated fields. There is lack of agreement whether these solitary males are territorial during summer (Kramer 1969; Schröder 1971). Understanding the causality of this general pattern is complicated by the often striking differences between populations.

I studied the late summer distribution of chamois *(Rupicapra rupicapra)* in the Bavarian Alps for the purposes of quantitatively describing dispersion and habitat use of group types and for testing the hypothesis that solitary males exclude other population members from the best feeding areas.

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The study area

The study area was the Kühalpenbach Valley; a side valley of the longer Graswang Valley located 100 km south of Munich in the Ammergauer Mountains. The topography varies from cliff-rimmed, high alpine cirques to gently sloping spruce and mixed spruce-beech-fir forest. The study area is approximately 625 ha in vertically projected area and varies in elevation from 1,000 to 1,943 m. A more detailed description of the general area is found in v. ELSNER (1980, 1982).

The study area has a long history of domestic stock pasturing and forestry. It has long been a favoured royal hunting area and 'Hege', the German concept of intensive game management, has been practiced for many years (HIECKE et al. 1981). In medieval times, the high elevation forest was cut-over to provide sheep, goat and cattle pasture thereby permanently altering the timberline. With the relaxation of grazing pressure in the past century, many of the Alps have reverted to 'Latschen'; a disclimax, snow resistent, recumbent pine *(Pinus mugo)*. There have been virtually no natural chamois predators in the study area for more than a century. At present, approximately 30 cattle are pastured in the valley from July to early October mostly in the forest openings and in meadows near timberline. Logging is on a small scale with cut-over areas allowed to naturally regenerate. Regular winter-feeding of red deer *(Cervus elaphus)* was instituted in the 19th century and currently maintains the species at high density resulting in heavy pressure on the forest ground vegetation. During the summer months, the valley is a popular hiking area.

The number of chamois using the study area, but not totally contained within it, was estimated at 150–250. Approximately 20 animals are shot yearly by the local professional hunter (Berufsjäger) and his officially-guided guest hunters. The history of hunting in the immediate area is reviewed in HIEKE et al. (1981).

Methods

To document chamois distribution, the study area was repeatedly traversed on foot between 27 July and 10 October, 1981. During these walks, 151 groups were classified by type, located on a 1:25,000 scale topographic map (Map No. 8432, Bayerisches Landesvermessungsamt, München). Use of an altimeter improved the accuracy of the location by allowing one certain 'fix'. Each day's walking route was marked on the map. Sightings were grouped into 100 m elevation intervals.

The study area was classified into seven different habitat types; 'Latschen', scree, cliffs and rock, forest, clear-cuts and their edges, meadows ungrazed by domestic animals, and meadows grazed by cattle. The relative proportions of these habitat types were determined by placing a regular dot grid over the map.

Expected habitat use was calculated for each habitat type as the sum, over all elevations, of the occupation of each elevation zone by a group type multiplied by the proportion of that habitat found at each elevation:

$$E_{gi} = \sum_{e=1,8} (P_{ge} \times H_{ie})$$

where E_{gi} = expected proportion of use by group type g of habitat type i, P_{ge} = proportion of group type g found in elevation zone e, and, H_{ie} = proportion of habitat type i in elevation zone e. This index implies that habitat choice is made solely within elevation intervals. It is therefore a conservative index of choice; that is, if elevation zones are partially chosen because of the availability of a particular habitat type, then choice is greater than reflected by the index.

Strength of habitat preference or rejection was calculated as:

$$P_{gi} = \frac{O_{gi} - E_{gi}}{E_{gi}}$$

where P_{gi} = the preference for habitat type by group type g, and where O_{gi} = the observed percentage of use of habitat type i by group type g. This index varies between -1 and $+\infty$.

Determinations of forage plant biomass were made in major habitat types by clipping herbaceous material from 20 × 50 cm (0.1 m^2) quadrats placed 5 m apart along a tape laid parallel to the slope. Samples were oven-dried at 60 °C for 18 h and weighed to the nearest 0.1 g.

An index of food quantity at a given elevation (Q_e) was calculated as:

$$Q_e = \sum_{i=1,6} (H_{ie} \times B_i)$$

where Q_e is an index of good quantity at elevation e, H_{ie} is the proportion of habitat i at elevation e, and B_i is the mean biomass per m^2 in habitat type i.

To examine relative densities between altitude zones, I calculated as an index of density, the number of individual animals seen per 100 m that I walked within each 100 m elevation zone. Below timberline, visibility is fairly uniform and the results are comparable between elevation zones. Above timberline, the open slopes afford high visibility and greater ease in sighting animals. Consequently, the analysis was restricted to individuals observed below timberline.

In all statistical tests, the 5 % level of probability was defined a priori as representing significance.

Results

Spatial distribution of group types

Male groups were most often seen in the gently sloping forest near the head of the valley and female groups were usually encountered near or above timberline in a crescent-shaped area around the entire valley. By contrast, single males were not concentrated in any particular environment or site but were found distributed throughout the entire study area.

Figure 1 represents a frequency distribution of the three group types' occupation of 100 m elevation zones. It shows that the mean elevation of occupation of single males (1424 m) and male groups (1440 m) is essentially identical whereas the mean elevation of female groups (1626 m) is much higher. However, there are obvious differences between single males and male groups. Single males occupy both the highest (1750–1850 m) and lowest (1150 m) elevation zones whereas male groups were found in neither. The coefficient of variation for single males (10.4) is higher than for male groups (7.8) indicating that male groups are more concentrated in the mid-elevation zones.

The variety in elevations occupied by the three group types can be expressed by the Shannon-Wiener index of diversity (Poole 1974, p. 391). Diversity of elevation occupation was 1.7 for single males, 1.4 for male groups, and 1.1 for female groups. Single males were significantly different in elevation diversity than male groups ($t = 2.007$, d.f. = 89) and female groups ($t = 2.933$, d.f. = 40) but the elevation diversities of male groups and female groups were not significantly different ($t = 1.531$, d.f. = 49). Single males were more evenly distributed over all elevations than were male groups and female groups.

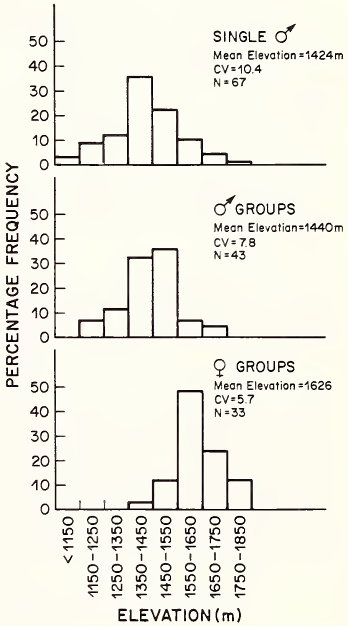
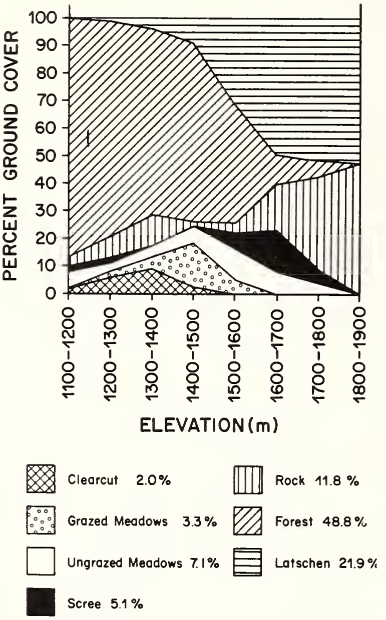


Fig. 1. Percentage of single males, male groups, and female groups observed at 100 m elevation intervals. CV = coefficient of variation around mean elevation of occupation

Habitat availability and choice

Throughout the entire study area, forest was by far the most common habitat type (49 %) followed by 'Latschen' (22 %) and cliffs-rock (12 %) (Fig. 2). The proportions of habitat types varied widely with elevation (Fig. 2). Figure 3 presents the pattern of habitat use exhibited by the three group types. Single males were most often observed in the forest, male groups in and around clear-cuts and female groups were most commonly seen in the 'Latschen'. The only habitat type used more than 20 % of the time by all group types was the 'Latschen'. The pattern of habitat use (Fig. 3) was significantly different between all group types (single male vs. male group, $\chi^2 = 61.3$; single male vs. female group, $\chi^2 = 217.5$; male group vs. female group, $\chi^2 = 404.9$, all with 6 d.f.).

Fig. 3 shows that 'Latschen' was preferred and forest was avoided by all group-types. Chi-square values comparing the observed and the expected are 33.9 for single males, 288.0



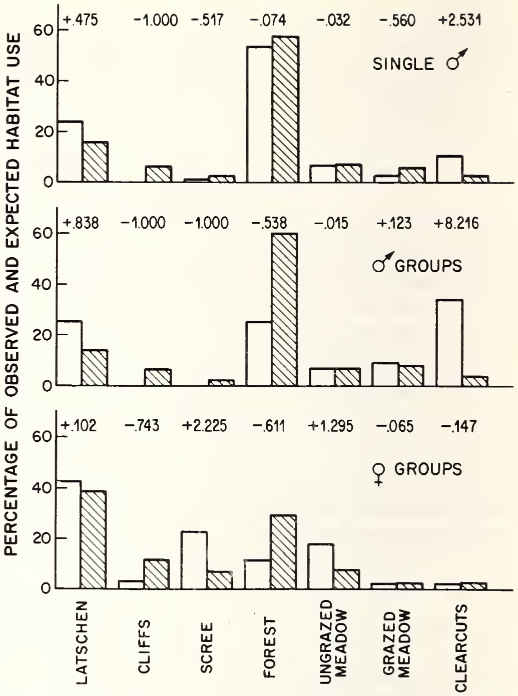


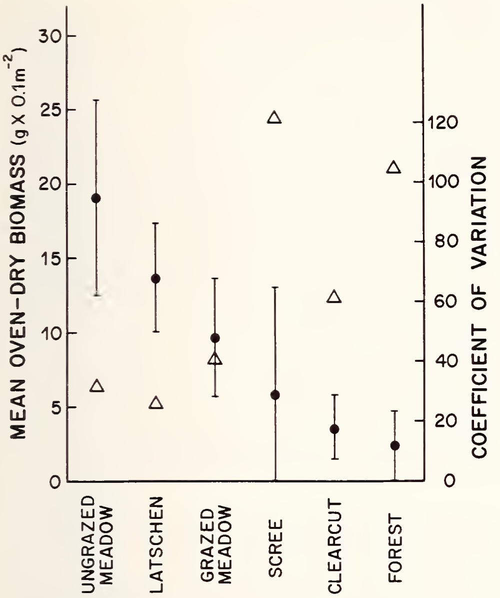
Fig. 2. Percentage ground cover of 7 different habitat types at 100 m elevation intervals. – *Fig. 3.* Observed and expected use of 7 habitat types by single males, male groups, and female groups. Open bars are observed percentage use; diagonally shaded bars are expected percentages. See text for method of calculating expected use. The number above the bars represents the strength of habitat preference or rejection (−1 to +∞). See text for method of calculation

for male groups, 288.0 for male groups, and 65.9 for group females (all with 6 d.f.). The differences are all statistically significant and suggest that single males are the least selective of habitat within their chosen elevation of occupation and male groups are by far the most selective. The high degree of choice exhibited by male groups arises primarily through avoidance of forest and attraction to openings.

Nutritional suitability of group ranges

The nutritional suitability of a range is composed of two aspects; food quality and food quantity. Atzler (1978) compared forage quality at three elevations in the Kühalpenbachtal (1040 m, 1350 m, and 1550 m) on eight occasions between May and October. He found dry matter and raw fibre contents to be negatively correlated with increasing elevation whereas most minerals, starch and raw protein all increased in content with increasing elevation. Between June and October, in vitro digestibility at 1550 m was found to be, on average 8.9 % higher than at 1040 m and 4.7 % higher than at 1350 m (paired t-tests on reported digestibilities; 1040 vs. 1350 m, $t = -16.58$; 1040 vs. 1550 m, $t = -6.65$; 1350 vs. 1550 m, $t = -4.81$; all with 5 d.f.; all significant, statistics by Shank). The quality of the forage in the study area would appear to increase with elevation. In North America, Johnston et al. (1968) and Hebert (1973) both report the same phenomenon and it is likely to be universal.

To examine whether forage quantity might be instrumental in elevation and habitat choice, I clipped the vegetation in 0.1 m^2 quadrats. Figure 4 presents the mean and



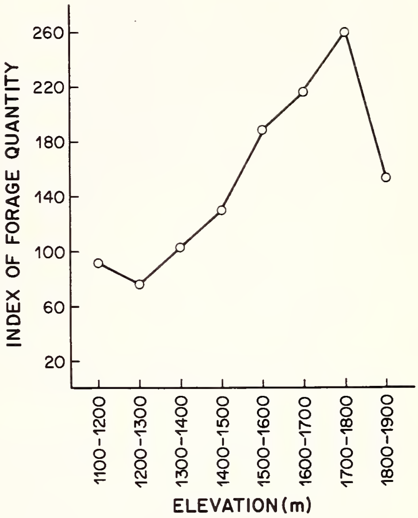


Fig. 4. Forage biomass (g · 0.1 m^2) in 6 habitat types (filled circles). The vertical bars represent standard deviations. The open triangles are coefficients of variation and are indicative of patchiness. – *Fig. 5.* Index of forage quantity at 100 m elevation intervals. See text for method of calculation

coefficients of variation of oven-dry biomass in the various habitat types. The figure shows that the open habitat types are the most heavily vegetated and generally the least patchily distributed (except scree).

Figure 5 presents Q_e, the index of food quantity and shows that greater plant biomasses are available to chamois at higher elevations except in the highest zone where barren cliffs predominate. Correlation coefficients were calculated between habitat use by the three group types (Fig. 3) and mean plant biomass in each habitat type (Fig. 4). For single males the correlation was −0.373 for male groups it was −0.383 and for female groups the coefficient was +0.446. None of these individual values is statistically different from zero but together they indicate a clear trend of biological significance; i.e., males trend to utilize habitat types with less food whereas females utilize habitats containing more food.

Density as a function of altitude

Figure 6 represents the index of chamois density at various elevations and shows a linear increase in density with increasing elevation. As mentioned above, this conclusion refers only to areas below timberline.

Discussion

The results suggest that single males are the most widely dispersed group type and occur most commonly throughout all elevation zones, in all portions of the study area and in all habitat types. Only single males occupy the lowest elevation zone. By contrast, male groups occupy primarily the mid-elevations and are the most limited group type with respect to dispersion and habitat occupation. Female groups occupy higher elevations than other group types but are widely dispersed within this zone. The degree of habitat choice

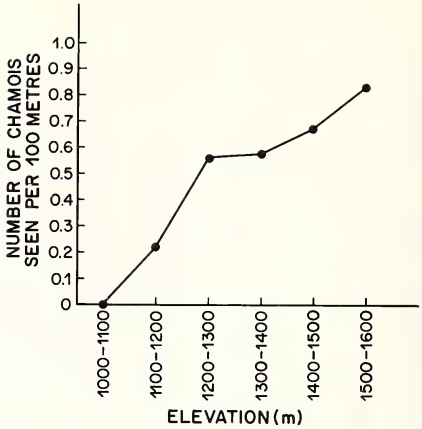


Fig. 6. Number of chamois seen per 100 m walked at 6 elevation intervals

exhibited by females is intermediate between single males and male groups. Population density appears to increase with elevation, at least below timberline.

It was hypothesized that the ecological and distributional differences between males and females, which are mostly attributable to differences in the elevation zones occupied, might be caused by intraspecific competition for limited food resources. Schröder (1971) presented data demonstrating that summer weight gains and rutting weight losses are far greater in males than in females and that these gains and subsequent losses increase in males up to age 6. It is therefore reasonable to expect that a male's rutting success and post-rut survival is dependent upon the adequacy of summer feed and that dominant males might exclude subordinate males and all females from the most favourable feeding areas. This hypothesis would accord well with Knaus and Schröder's (1975) suggestion that some males are territorial during the summer. If the food hypothesis is correct, one would expect to find better feeding conditions at lower elevations.

The summer forage resources available to female groups is superior in quality and quantity relative to that available to males. This is contrary to the hypothesis that males exclude females from the best feeding areas, as occurs in Downy Woodpeckers *(Picoides pubescens)* (Peters and Grubb 1983). It suggests either that males are altruistically allowing females to use the better areas (Geist and Petocz 1977; Watson and Staines 1978) or that males have requirements differing from those of females (Clutton-Brock et al. 1982).

Schröder (1971) presented data showing that single males in the Hochschwab Range (Steiermark, Austria) were distributed with mean elevations of occupation several hundred m lower than group-living males. Such a pronounced separation was not found in the Kühalpenbachtal (Fig. 1) although only single males occupied the lowest elevation zone and the single male frequency distribution was skewed toward lower elevations. Striking variation in patterns of range occupation and behaviour, both within and between populations, is common in chamois.

I herein propose that differences between areas in degree of segregation of solitary males from group males are explainable by reference to a simple and testable two-factor optimization model. The model assumes that single males choose an elevation of occupation which represents a compromise between requirements for adequate food resources and sufficient solitude. This "need for solitude" is hypothetical and purposely vague but appears to reflect the social intolerance and irritableness exhibited by single males (e.g. see Kramer 1969). The solitude requirement is not considered to be a trait in itself but as the manifestation of underlying adaptations; perhaps a tendency to avoid energy-consuming social interaction.

The model assumes two conditions. First, that the quantity and/or quality of food resources is directly proportional to elevation. And second, that chamois distribute themselves vertically in densities roughly proportional to the availability and quality of food; that is, density is directly proportional to elevation (see FRETWELL and LUCAS 1970). Both of these assumptions are supported by the results presented above.

Figure 7A depicts the costs and benefits accruing to a single male by moving to a higher elevation under conditions of good and poor food and of high and low density. For example, if food is poor (LOW F), a male located at low elevation will gain a great deal in improved feeding conditions by moving to a higher location. However, if population density is high (HIGH D), a move to higher elevation will entail a high cost in reduced solitude. The elevation at which the male should settle is that at which costs and benefits cancel out (vertical dotted lines). Moving either up or down the mountain from this optimal elevation will result in a loss of net benefit.

Figure 7B depicts the difference between cost and benefit accruing to a single male by moving to a higher elevation. The optimal elevation is that at which there is no net benefit to moving higher. If the single male is located at an elevation higher than the optimal, by moving to a lower altitude he gains more in solitude than he loses in solitude. Conversely, if he is higher than the optimal, by moving uphill, he gains more in food than he loses in solitude. The slope of the net benefit lines represent the increment in net benefit per unit elevation change. Where slopes are high, the single male loses more per unit deviation from the optimal than where slope are low. Hence, the variance in elevation zone occupation should be larger when the net benefit slopes are lower.

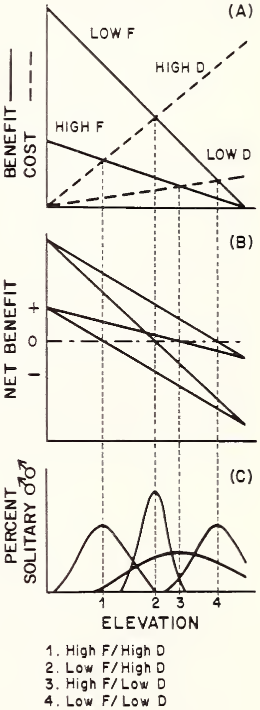


Fig. 7. Graphical representation of an optimization model predicting the altitudinal distribution of solitary male chamois. In A, the solid lines indicate the benefits in enhanced food gained by a single male which moves to an incrementally higher elevation. The dashed lines represent the costs in reduced solitude by making such a move. In B, the lines represent the net benefit (benefits less costs) entailed in moving to an incrementally higher elevation. Higher slopes entail greater losses in net benefit per unit deviation from the optimal altitude. In C, the frequency distributions predicted under the 4 regimes of food and population density are depicted. The areas under the curve are all equal but the amplitudes and variances differ

Figure 7C depicts the frequency distributions of elevation occupation by solitary males under the four combinations of food and population density. The model predicts that areas with distinct elevational separation between solitary and group-living males, such as the Hochschwab Range (SCHRÖDER 1971), should have dense populations of chamois on excellent range. By contrast, where solitary males overlap greatly with group-living males and occupy almost all elevational zones, such as in the Kuhalpenbachtal, range conditions should also be excellent but the population density relatively low. Where all chamois in the population inhabit only the best habitat, such as occurs in many low, forested mountains of central Austria, both population density and food resources are predicted to be poor. Under conditions of poor food and high density, the luxury of solitary-living might be abandoned althogether and consequently, the predicted low-variance distribution at mid-altitude might never be in evidence.

This model is a priori in nature and must be tested to determine how well it accords with reality.

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Zusammenfassung

Inter- und intra-sexuelle Segregationen von Gemsen (Rupicapra rupicapra) im Sommer in Abhängigkeit von Höhenlage und Habitat

Die spätsommerliche Verbreitung von Gamswild *(Rupicapra rupicapra)* wurde in den Bayerischen Alpen quantitativ erfaßt. Man notierte Verbreitung, Höhenlage und Biotopauswahl der Geißen und Bockrudel sowie der einzelstehenden Böcke. Die Pflanzenmasse wurde für jeden wichtigen Biotop an Hand von 0,1 m^2 Quadraten, welche sorgfältig gemäht wurden, berechnet. Die Geißen hielten sich in den höchsten Höhenlagen auf. Die durchschnittliche Höhenlage der Standorte einzelstehender und rudelbildender Böcke war die gleiche, allerdings fand man einzelstehende Böcke über eine größere Höhenlage verstreut. Einzelgänger waren betreffs Biotop weniger wählerisch als Gamsböcke in Rudeln. Qualität und Quantität der Äsung waren positiv mit der Höhenlage korreliert. Die Hypothese, daß Böcke Geißen aus den besten Äsungsgebieten verdrängen, ist somit widerlegt. Es wird ein Modell besprochen, das auf dem Konflikt zwischen der Wahl besserer Äsung und der Wahl ruhiger Einstände fußt. Dort wo Äsung im Überfluß vorhanden und der Bestand sehr dicht ist, erwartet man, daß sich einzelne Böcke in den tieferen Höhenlagen aufhalten und sich nur wenig in ihren Standorten mit anderen Gemsen überschneiden. Ist die Äsung reichlich, aber die Populationsdichte gering, erwartet man, daß einzelne Böcke über eine breite Zone der Höhenlagen verbreitet sind, und daß sich ihre Standorte mit anderen Gemsen überschneiden.

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WISSENSCHAFTLICHE KURZMITTEILUNG

Tagesschlaflethargie bei der gelbfüßigen Breitfußbeutelspitzmaus, *Antechinus flavipes* (Marsupialia: Dasyuridae)

Von F. GEISER[1]

School of Biological Sciences, Flinders University, Bedford Park, Adelaide, Australia

Eingang des Ms. 16. 1. 1985

Körpertemperaturmessungen an der gelbfüßigen Breitfußbeutelspitzmaus, *Antechinus flavipes* (MORRISON 1965) zeigten nur kleine tägliche Schwankungen und veranlaßten TYNDALE-BISCOE (1973) zur Annahme, daß diese Art, im Gegensatz zu verschiedenen anderen

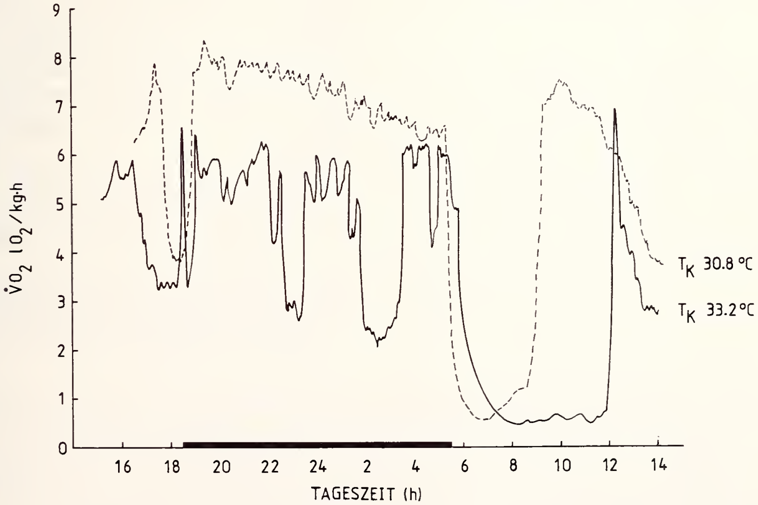

Abb. 1. Der Tagesverlauf des Sauerstoffverbrauchs ($\dot{V}O_2$) von *Antechinus flavipes* A (Gewicht 26 g) bei Umgebungstemperaturen von 17,1 (——) und 12,0 °C (– – –). Dunkelheit ist mit einem schwarzen Balken angezeigt. Körpertemperaturen (T_K) wurden am Ende der Experimente gemessen und sind in °C angegeben

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