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Effects of weather and season on the summer activity of dormice *Muscardinus avellanarius*

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(With 2 figures in the text)

Activity schedules of dormice were investigated in relation to weather and seasonal factors, by automatic monitoring of temperatures in nests of free-living animals. Data were obtained for two years and 294 dormouse-nights. The principal exogenous factor influencing pan-seasonal activity was photoperiod, activity beginning about 30 min after sunset and ending about 50 min before sunrise. However, on a seasonal scale, activity start time, end time and length were all strongly affected by ambient temperature and rainfall; higher temperatures appeared to lengthen activity, whereas rainfall reduced it. Diurnal activity was rare and took place when ambient air temperatures at midnight fell below 9 °C. There were large differences in activity schedules between years, which were also correlated with weather conditions. Dormice are thus directly affected by weather, which also strongly influences the availability of their food. Weather may in general heavily influence small hibernators, because they can utilise facultative torpor to overcome adverse conditions. Our results imply that weather may have a profound effect on dormouse life history, especially in Britain's maritime climate where summers are frequently cool and wet.

Contents

Introduction

The activity patterns of small endotherms are known to be strongly influenced by ambient weather conditions (Erkert, 1982; Elkins, 1983), as a result of these animals having low thermal inertia and limited energetic autonomy (McNab, 1983; Genoud, 1988). The response of small mammalian hibernators, like the dormouse *Muscardinus avellanarius*, to adverse summer weather, such as low ambient temperatures and rainfall, may be especially pronounced. This is because hibernators are not obliged to forage during adverse conditions, but can greatly reduce their activity and compensate for the ensuing lower energy gain from foraging by utilizing facultative torpor. There have been few studies examining the influence of weather on summer activity in free-ranging hibernators (e.g. Laufens, 1973; McAney & Fairley, 1988; Maier, 1992). Previous studies of dormouse summer activity have been conducted under captive conditions (Walhovd, 1971) or have been largely unquantified and involved very small samples of animals (Laufens, 1975). No studies have examined the influence of weather on dormouse activity, but observations of radio-tagged dormice suggested that it strongly influenced activity (Bright & Morris, 1991). This paper reports a study of free-living dormice in the non-hibernal period, i.e. from May to early November, using an automatic monitoring technique. It aims to determine the effects of weather on activity and assess how these change throughout the summer.

Study area

The study was conducted in a 4.5 ha section of a larger area of deciduous, low-growing woodland in Somerset; a more extensive but otherwise similar area to that described by Bright & Morris (1991, 1993). Briefly, the site is at an altitude of 150–200 m O.D. in a steep-sided limestone valley. Hazel *Corylus avellana* is the predominant understorey shrub, occurring with hawthorn *Crataegus monogyna*, blackthorn *Prunus spinosa*, wayfaring tree *Vibernum lantana*, dogwood *Thelycrania sanguinea* and yew *Taxus baccata*. Ash *Fraxinus excelsior*, sycamore *Acer pseudoplatanus* and whitebeam *Sorbus anglica* occur as occasional emergents from the understorey. The site supports a high density of dormice (*c.* 10/ha^{-1}) most of which use specially provided nestboxes (Bright & Morris, 1990; Morris, Bright & Woods, 1990).

Methods

Monitoring activity

Activity was monitored using thermistors placed in nests within nestboxes. Thermistors were linked to an array of dataloggers (Squirrel meter/loggers, Grant Instruments, Cambridge) which recorded ambient temperatures and those within nestboxes every 5 min, to an accuracy of 0.2 °C. Graphs of nest and ambient temperature against time were used to determine the timing of dormouse activity. An initial rapid fall in nest temperature (-5 °C/5 min), followed by slower cooling to within 2 °C of ambient air temperature, indicated that a dormouse had left its nest. Conversely, a rapid rise in nest temperature ($>$ 5 °C/5 min) from close to ambient air temperature, indicated when a dormouse returned to its nest. On 11 occasions ($n = 8$ individuals) when exact times of leaving and returning to nests were known from radio-tracking, there was complete correspondence between these times and those derived from nest temperature records; validating our interpretation of the latter. (There were few records of exact activity timing from radio-tracking because a discontinuous sampling programme was used; Bright & Morris, 1991.)

We assumed that activity records from a nestbox in any one night were for the same dormouse, as radio-tracking at the study site (Bright & Morris, 1991) showed it was very unlikely that a different dormouse would move into a nest on the night that it had been vacated. Dormice are often found sharing nests (Morris *et al.*, 1990), and some activity records clearly showed 2 non-synchronous episodes of rapid nest cooling and rapid nest warming. Radio-tracking confirmed that dormice sharing a nest began and ended their activity at different times, so data from them were treated as independent. In these cases, we assumed, in the light of radio-tracking observations, that the first dormouse to leave a nest was also the first one to return to it. Dormice were individually marked by fur-clipping, during monthly or, where necessary, 2-weekly nestbox inspections. This was a more intensive monitoring programme than for parallel radio-tracking studies (Bright & Morris, 1991). However, when 2 dormice shared a nestbox it was not possible to determine from temperature recordings which individual was responsible for a particular activity record. In these cases, the sex of a dormouse and its individual identity were treated as missing values in analyses.

Weather data

Air temperature at 00:00 h was recorded near nestboxes at 1.5 m above ground level. Data on rainfall (of 1 mm or more) and cloud cover (in oktas, or eighths of the sky covered) were obtained from Meteorological Office weather stations 4.5 km (rainfall) and 10 km (cloud cover) from the study site. Rainfall data referred to 24-h periods beginning at 09:00 h, not only night-time when dormice were active. Data for cloud cover were for the period 19:00 to 04:00 h. Dates when the moon was visible above the horizon at night and moonphase were taken from Whitaker's Almanac (Anon., 1987, 1988) and used to calculate a moonlight index for each night: moonlight index = (1/cloud cover) × moonphase.

Analytical approach

We first examined the influence of sunset and sunrise on activity patterns over the whole summer, pooling data for 1987 and 1988 when it became clear that the whole-summer patterns of activity were very similar between years. Subsequent analyses examined activity by seasons, that were chosen to reflect dormouse life history and feeding behaviour (Bright & Morris, 1993):

Season 1: May–June, usually prior to breeding, when dormice feed mainly on tree flowers.
Season 2: July–August, during the breeding period, a time of transition from food scarcity to food abundance.
Season 3: September–early November, after the birth of most young, when dormice feed on an abundance of autumn fruits.

Analyses of variance (ANOVAs) were used to partition variance in activity between individuals, between years, and that due to environmental factors. ANOVAs were run excluding some covariates or factors, to examine the degree to which autocorrelation between variables affected final models. We also checked that the assumptions of ANOVA were met (Sokal & Rohlf, 1981), particularly homogeneity of group variances. An arcsin transformation was applied to the moonlight index and a square root transformation to the rainfall data, to normalize them before analyses.

Results

Data were obtained for 294 dormouse-nights (plus further nights for a lactating female, see below), representing nine dormice sampled in May–June, 11 in July–August and seven in September–early November.

Pan-seasonal activity patterns

The times of start and end of activity each month were closely correlated with sunset and sunrise, respectively (product-moment correlation, $P < 0.001$ in both cases), so that activity length was short in mid-summer and increased in the autumn (Fig. 1). Dormice became active at a mean of 28.8 min (S.E. 10.5) after sunset. The difference between sunset and activity start time varied significantly between individual dormice but not between months (ANOVA: for individual $F_{1,277} = 6.11$, $P = 0.01$; for month $F_{6,277} = 1.27$, $P = 0.27$). Activity ended at a mean of 49.5 min (S.E. 11.5) before sunrise. The difference between activity end time and sunrise did not vary significantly between individuals, but did so between months (ANOVA: for individual $F_{1,268} = 2.97$, $P = 0.86$; for month $F_{6,268}$, $P = 0.04$). Relative to sunrise, dormouse activity ended earlier in September than in other months (Tukey's test, $P < 0.05$).

Activity was always unimodal, with the exception of one female monitored during early lactation who returned to her nest for 20–35 min between 00:00 h and 02:00 h (11 nights of recording in August; for clarity these data were excluded from ANOVAs). Otherwise, the activity schedules of male and female dormice, including females in later lactation, appeared identical at all seasons (Tables I, III). Radio-tracking (cf. Bright & Morris, 1991) showed that dormice did not usually cease activity when away from nests.

There was no significant variation in activity start time between individual dormice during different seasons (Tables I–III). However, activity end time and length did vary significantly between individuals during September–early November (Table III), when the length of the night was longer.

Influence of temperature on activity

In May–June, higher ambient temperatures were positively correlated with activity start time and activity end time; activity length increased at a rate of 6.2 min/°C (Table I; activity increase estimated from regression coefficient). Temperature was not related to activity length in July–August, though it did have a small, but statistically significant, effect on activity end time (Table II). In September–early November, temperature was again strongly positively correlated with activity length, which increased at a rate of 13.3 min/°C (Table III). Times of activity start and end were, however, highly variable during this season (Fig. 1) and, as a consequence, not related to temperature.

Influence of rainfall and moonphase on activity

In May–June, rainfall was negatively correlated with activity start time and activity length; rainfall appeared to reduce activity length by −3.0 min/mm rainfall (Table I). There was no significant relationship between activity and rainfall in ANOVAs for other seasons (Tables II & III). However, the influence of rainfall may have been underestimated, as may that of moonphase which was not related to any measures of activity (see *Differences in activity between years* and **Discussion**).

Diurnal activity

Dormice were active during daylight hours on only 28 (9.5%) dormouse-days of recording and then only between 12:00 h and sunset, the warmest time of the day. Diurnal activity lasting more than 30 min took place on days when air temperature at midnight fell below 9 °C (Fig. 2). Its length was negatively correlated with air temperature at midnight, but not other covariates (ANOVA: for temperature $F_{1,17} = 25.48$, $P < 0.001$; for moon index $F_{1,17} = 0.25$, $P = 0.62$; for rainfall $F_{1,17} = 2.50$, $P = 0.13$; for individual $F_{1,17} = 0.71$, $P = 0.40$). In September–early November 1988, when air temperatures were low (Table IV), diurnal activity was most frequent

TABLE I

*ANOVAs of factors affecting activity start time, activity end time, and activity length (in hours BST) during May–June. The variance ratio (F), for each covariate or factor is given (**d.f.** 1,59). Probability (**P**) values are shown as: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Standardized regression coefficients (b) follow significant covariates and there were no significant interactions between the factors*

	May–June								
	Activity start time			Activity end time			Activity length		
Source of variation	F	*P*	b	F	*P*	b	F	*P*	b
Covariates									
Temperature at 00:00 h	7.22	**	0.050	10.81	***	0.055	18.43	***	0.104
Moon index	0.02			0.26			0.05		
Rainfall	5.67	*	− 0.037	0.81			5.92	**	− 0.05
Night length	0.51			2.27			2.48		
Individual	1.82			0.73			0.20		
Sex	0.05			0.00			0.05	**	
Year	5.32	*		2.19				0.56	

and lasted longer than at other seasons (ANOVA: for season $F_{3,17} = 0.37$, $P = 0.69$; for year $F_{1,17} = 1.69$, $P = 0.21$; for year × season interaction $F_{2,17} = 3.69$, $P = 0.04$; followed by Tukey's test, $P < 0.05$).

Differences in activity between years

There were significant differences in activity schedules between 1987 and 1988, apparently related to weather conditions. Ambient temperatures (measured at midnight) were significantly higher during May–June 1988 than during the same period in 1987 (Table IV; Tukey's test

TABLE II

*ANOVAs of factors affecting activity start time, activity end time and activity length (in hours BST) during July–August. The variance ratio (F) for each covariate or factor is given (**d.f.** 1,63). Probability (**P**) values are shown as: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Standardized regression coefficients (b) follow significant covariates and there were no significant interactions between the factors. Note that night length is highly significant in ANOVAs for this season, because there was a much greater range of night lengths*

	July–August								
	Activity start time			Activity end time			Activity length		
Source of variation	F	*P*	b	F	*P*	b	F	*P*	b
Covariates									
Temperature at 00:00 h	0.89			7.34	**	0.037	0.97		
Moon index	1.40			1.50			2.53		
Rainfall	1.14			0.01			0.47		
Night length	41.49	***	− 0.383	45.81	***	0.347	75.82	***	0.729
Individual	0.02			3.26			1.00		
Sex	0.17			1.29			0.16		
Year	3.04			23.78	***		17.81	***	

TABLE III

*ANOVAs of factors affecting activity start time, activity end time and activity length (in hours BST) during September–early November. The variance ratio (F) for each covariate or factor is given (**d.f.** 1,94). Probability (**P**) values are shown as *P <0.05, **P <0.01, ***P <0.001. Standardized regression coefficients (b) follow significant covariates and there were no significant interactions between the factors*

	September–early November								
	Activity start time			Activity end time			Activity length		
Source of variation	F	*P*	b	F	*P*	b	F	*P*	b
Covariates									
Temperature at 00:00 h	2.44			1.95			10.10	**	0.223
Moon index	1.17			1.68			0.67		
Rainfall	0.04			0.04			0.46		
Night length	0.61			1.49			4.38	*	0.526
Individual	3.31			5.38	*	0.020	6.53	*	0.014
Sex	1.84			0.02			0.48		
Year	7.65	***		0.82			0.25		

$P < 0.05$). In 1988, dormice began their activity significantly earlier (Table I, year significant; 1988: 21:43 h S.E. 12.8 min vs. 1987: 22:08 h S.E.17.0 min). In 1988, ambient temperatures during September–early November were significantly lower than in 1987 (Table IV; Tukey's test $P < 0.001$). However, in this case, lower temperatures were positively correlated with activity start time (Table III, year significant; 1988: 17:28 h S.E. 30.9 min vs. 1987: 19:52 h S.E. 5.2 min). We suggest that this was because mean temperatures in 1988 were below the 9 °C threshold that appears to stimulate diurnal activity (cf. Fig. 2).

Rainfall was higher during July–August 1988 (Table IV; Tukey's test $P < 0.001$), when activity end time was significantly earlier and activity length significantly shorter (Table II, year significant; activity end time: 1988: 04:15 h S.E. 5.4 min vs. 1987: 04:40 h S.E. 4.0 min; activity length 1988: 6 h 18 min S.E. 9.1 min vs. 1987: 7 h 10 min S.E. 6.9 min). We suggest that these differences were due to rainfall, even though it was not directly related to activity (Table II). This is because rainfall covaried with year and, removing the year term from the ANOVA, resulted in a significant effect of rainfall ($P < 0.001$).

Discussion

Monitoring nest temperatures gave a precise measure of dormouse activity, without influencing the animal's behaviour. Very brief (< 5 min) returns to the nest during the night might not have been recorded using this method, but simultaneous radio-tracking at the study site (Bright & Morris, 1991) showed that these were very infrequent at all seasons (recorded in only six of 183 dormouse-nights). Laufens (1975) described such returns as frequent in autumn.

Dormice were strongly nocturnal, as commonly suggested (Barrett-Hamilton & Hinton, 1910–1921; Laufens, 1975). Except on cold nights, activity began about 30 min after sunset and was closely correlated with it. As in small rodents, bats (e.g. Voûte, Sluiter & Grimm, 1974; Wolton, 1983), and captive dormice (Walhovd, 1971), the time of activity end was more variable, though still correlated with sunrise. Photoperiod was thus the principal exogenous factor affecting dormouse activity at a seasonal level, but activity was also strongly influenced from night to night

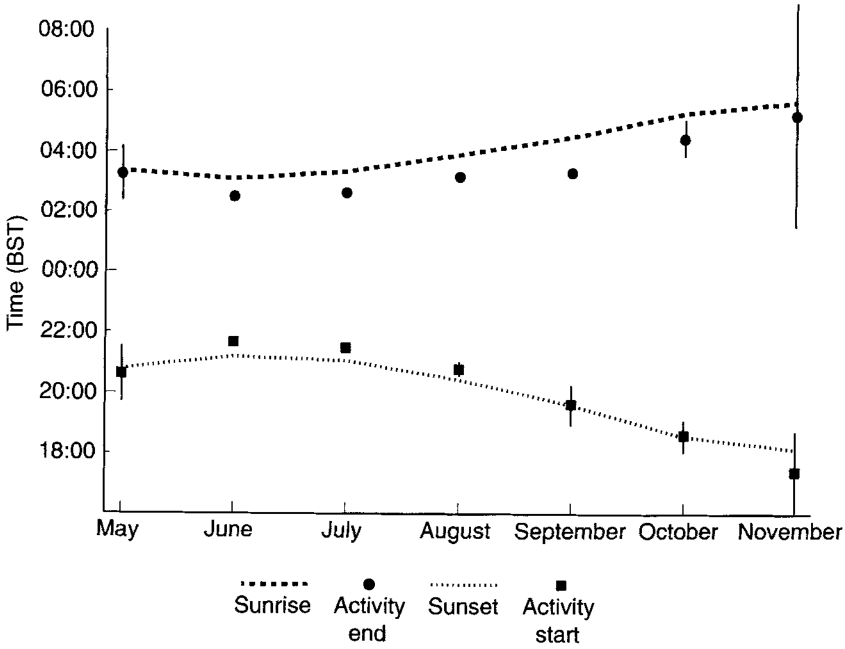

FIG. 1. Monthly changes in activity start time and activity end time (British Summer Time, BST), in relation to sunset (dotted line) and sunrise (dashed line). Means and standard errors are shown based on data pooled for 1987 and 1988.

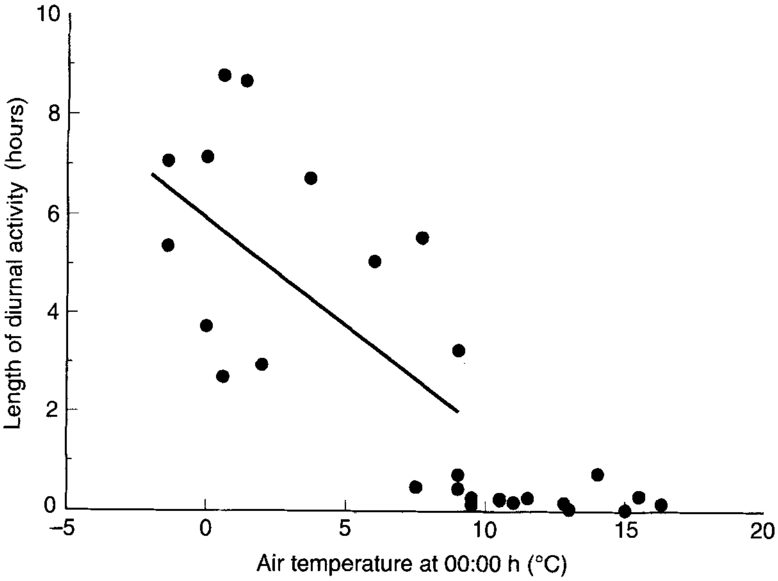

FIG. 2. The relationship between the length of diurnal activity and air temperatures below 9 °C at midnight. The line ($r^2 = 64.8\%$) was fitted by a regression which took the form: length of diurnal activity = $-0.435 \times$ air temperature $+ 5.920$.

TABLE IV

Seasonal change in daily ambient temperature at midnight (°C) and total daily rainfall (mm) in 1987 and 1988. Means for three seasons are shown, followed by standard errors in parentheses. ANOVA of temperature: for season $F_{2,288} = 36.29$, $\mathbf{P} < 0.001$*; for year* $F_{1,288} = 5.41$, $\mathbf{P} = 0.021$*; season × year interaction* $F_{2,288} = 11.94$, $\mathbf{P} < 0.001$*. ANOVA of rainfall: for season* $F_{2,288} = 2.58$, $\mathbf{P} = 0.077$*; for year* $F_{1,288} = 0.22$, $\mathbf{P} = 0.642$*; season × year interaction* $F_{2,288} = 3.07$, $\mathbf{P} = 0.048$

	Season					
	May–June		July–August		September–early November	
	1987	1988	1987	1988	1987	1988
Mean daily ambient temperature at 00:00, °C (S.E.)	9.53 (0.42)	11.40 (0.48)	12.03 (0.28)	11.60 (0.31)	8.81 (0.52)	4.49 (0.55)
Mean total daily rainfall, mm (S.E.)	1.37 (0.39)	1.69 (0.72)	1.54 (0.50)	3.27 (0.80)	1.68 (0.45)	1.28 (0.41)

by other factors. Rodolfi (1994) found no correlation between sunset or sunrise and fat dormouse *Glis glis* activity; this was probably because he did not record the time of activity start and end, only the presence of animals in feeding trees.

Dormice were active for most of the night except in September (Fig. 1), suggesting that short nights could have constrained activity between May and August, as appears to be the case with wood mouse *Apodemus sylvaticus* activity (Wolton, 1983). However, food shortage in mid-summer (Bright & Morris, 1993) might also have led to relatively extended periods of activity concomitant with finding sufficient food. In October, dormice were again active for nearly the whole night and radio-tracking showed that they were feeding intensively on hazelnuts prior to hibernation (Bright & Morris, 1993). Rodolfi (1994) found that fat dormice also showed increased activity before hibernation.

In contrast to studies of small rodents and some bats (Morrison, 1978; Erkert, 1982; Wolton, 1983; Scheibe, 1984), we found no relationship between dormouse activity and moonlight levels. This may be because moonlight was not measured directly, or it could be related to dormice foraging in thick arboreal cover (Bright & Morris, 1991; pers. obs.), where they would be mostly in deep shade, and possibly difficult for predators to detect, whatever the moon phase.

Lower temperature had the effect of shortening activity at all seasons, especially during May–June and September–early November when some nights were cooler. Similarly, temperatures below 9 °C at midnight led to diurnal activity, especially in autumn when activity lengths were long, associated with intensive pre-hibernal foraging. This accords with Millais' (1905) observation of diurnal activity in autumn and spring. By contrast, Laufens (1975) suggested that high ambient temperatures retard activity onset. However, his results are not likely to be representative, being based on a very small number of dormice sampled irregularly over six years. Studies on other small hibernators have shown that summer activity is markedly reduced during colder conditions (Erkert, 1982; Maier, 1992), and Wolton (1983) found that wood mice reduced their activity on colder nights, but at lower ambient temperatures (2–4 °C) than those we found to affect dormice.

Dormice thus appear to reduce activity to compensate for higher rates of heat loss at lower ambient temperatures and switch to diurnal activity when temperatures are especially low. We suggest that diurnal activity was less frequent in May–June because dormice compensate for low ambient temperatures at this time in a different way, by utilizing facultative torpor (P. W. Bright, unpublished data).

The activity of some small hibernators is known to be influenced by rainfall (Gaisler, 1963; Fenton *et al.*, 1977; McAney & Fairley, 1988), while others appear to be unaffected (Kunz, 1974; Swift, 1980). In the current study, rainfall reduced dormouse activity length slightly in May–June (1987 and 1988) and in July–August 1988. However, its influence may have been greater than suggested by the ANOVAs, because rainfall was autocorrelated with temperature, and removing the temperature term from ANOVAs usually resulted in rainfall becoming significant. Radio-tracking observations at the study site support this contention: on 26 dormouse-nights from May to October when there was rain, dormice returned to their nests at least one hour before the mean times of activity end shown in Fig. 1. During moderate or heavy rain the dormouse's fur can become waterlogged, perhaps due to its few guard hairs and very fine, dense underfur (pers. obs.). This would greatly increase rates of body heat loss, which the reduction in activity during rain may serve to ameliorate.

Weather conditions thus have a direct effect on dormouse nightly activity. They also strongly influence the availability and abundance of the dormouse's principal foods, tree flowers and fruits (Bright & Morris, 1993). We therefore suggest that weather may have a profound effect on dormouse life history, especially in Britain's maritime climate where summers are frequently cool and wet. In particular, the correlation between weather and large differences in activity in 1987 and 1988, imply that the timing of breeding could be greatly retarded and pre-hibernal foraging impaired by inclement weather, leading to lower recruitment and overwinter survival. Thus, the scarcity of dormice in Britain (Hurrell & McIntosh, 1984; Bright, 1995) may be partly a function of a maritime climate, in contrast to the continental climate prevailing over most of the dormouse's range in Europe.

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REFERENCES

Anon. (1987). *Whitaker's Almanac.* London: Whitaker.

Anon. (1988). *Whitaker's Almanac.* London: Whitaker.

Barrett-Hamilton, G. E. H. & Hinton, M. A. C. (1910–1921). *A history of British mammals.* London: Gurney & Jackson.

Bright, P. W. (1995). Distribution of the dormouse in Wales, on the edge of its range. *Mamm. Rev.* **25:** 101–110.

Bright, P. W. & Morris, P. A. (1990). Habitat requirements of dormice in relation to woodland management in south west England. *Biol. Conserv.* **54:** 307–326.

Bright, P. W. & Morris, P. A. (1991). Ranging and nesting behaviour of the dormouse, *Muscardinus avellanarius*, in diverse low-growing woodland. *J. Zool., Lond.* **224:** 177–190.

Bright, P. W. & Morris, P. A. (1993). Foraging behaviour of dormice *Muscardinus avellanarius* in two contrasting habitats. *J. Zool., Lond.* **230:** 69–85.

Elkins, N. (1983). *Weather and bird behaviour.* Carlton: T. & A. D. Poyser.

Erkert, H. G. (1982). Ecological aspects of bat activity rhythms. In *Ecology of bats*: 201–242. (Kunz, T. H. (Ed.)) New York: Plenum Press.

Fenton, M. B., Boyle, N. G. H., Harrison, T. M. & Oxley, D. J. (1977). Activity patterns, habitat use and prey selection by some African insectivorous bats. *Biotropica* **9:** 73–85.

Gaisler, J. (1963). Nocturnal activity of the lesser horseshoe bat, *Rhinolophus hipposideros. Zool. Listy* **12:** 223–230.

Genoud, M. (1988). Energetic strategies of shrews: ecological constraints and evolutionary implications. *Mamm. Rev.* **18:** 173–193.

Hurrell, E. & McIntosh, G. (1984). The Mammal Society Dormouse Survey, January 1975–April 1979. *Mamm. Rev.* **14:** 1–18.

Kunz, T. H. (1974). Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). *Ecology* **55:** 693–711.

Laufens, G. (1973). Einfluss der aussentemperaturen auf die Aktivitätsperiodik der Fransen- und Bechsteinfledermäuse (*Myotis nattereri*, Kuhl 1818 und *Myotis bechsteini*, Leisler 1818). *Period. biol.* **75:** 145–152.

Laufens, G. (1975). Beginn und ende der täglichen Aktivität freilebender Haselmäuse (*Muscardinus avellanarius* L.) und Siebenschläfer (*Glis glis*. L.). *Z. Saugetierk.* **40:** 74–89. (English summary.)

Maier, C. (1992). Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in Oxfordshire. *J. Zool., Lond.* **228:** 69–80.

McAney, C. M. & Fairley, J. S. (1988). Activity patterns of the lesser horseshoe bat *Rhinolophus hipposideros* at a summer roost. *J. Zool., Lond.* **216:** 325–338.

McNab, B. K. (1983). Energetics, body size, and the limits to endothermy. *J. Zool., Lond.* **199:** 1–29.

Millais, J. G. (1905). *The mammals of Great Britain and Ireland.* London: Longmans.

Morris, P. A., Bright, P. W. & Woods, D. (1990). Use of nestboxes by the dormouse *Muscardinus avellanarius*. *Biol. Conserv.* **51:** 1–13.

Morrison, D. W. (1978). Lunar phobia in a neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Anim. Behav.* **26:** 852–855.

Rodolfi, G. (1994). Dormice *Glis glis* activity and hazelnut consumption. *Acta theriol.* **39:** 215–220.

Scheibe, J. S. (1984). The effects of weather, sex and season on the nocturnal activity of *Peromyscus truei* (Rodentia). *SWest. Nat.* **29:** 1–5.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry.* New York: Freeman.

Swift, S. M. (1980). Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *J. Zool., Lond.* **190:** 285–295.

Voûte, A. M., Sluiter, J. W. & Grimm, M. P. (1974). The influence of the natural light-dark cycle on the activity rhythm of pond bats (*Myotis dasycneme* Boie, 1825) during summer. *Oecologia* **17:** 221–243.

Walhovd, H. (1971). The activity of a pair of common dormice *Muscardinus avellanarius* in conditions of captivity. *Oikos* **22:** 358–365.

Wolton, R. J. (1983). The activity of free-ranging wood mice *Apodemus sylvaticus*. *J. Anim. Ecol.* **52:** 781–794.