van Zyl, typing by S. Saven and M. Scheiner. J. A. J. Nel, M. L. Wilson and W. J. J. van Rijssen are thanked for comments on an early draft of this paper.

REFERENCES

Avery, G. (1984). Results of patrols for beached seabirds conducted in southern Africa in 1982. *Cormorant* **12:** 29–43.

Avery, G. (1985). Results of patrols for beached seabirds conducted in southern Africa in 1983. *Cormorant* **13:** 3–15.

Avery, G., Avery, D. M., Braine, S. & Loutit, R. (1984). Bone accumulation by hyaenas and jackals: a taphonomic study. *S. Afr. J. Sci.* **80:** 186–187.

Avery, G. & Underhill, L. G. (1986). Seasonal exploitation of seabirds by Late Holocene coastal foragers: analysis of modern and archaeological data from the western Cape, South Africa. *J. archaeol. Sci.* **13:** 339–360.

Bridgeford, P. (1985). Unusual diet of the lion *Panthera leo* in the Skeleton Coast Park. *Madoqua* **14:** 187–188.

Brooke, R. K., Cooper, J., Shelton, P. A. & Crawford, R. J. M. (1982). Taxonomy, distribution, population size, breeding and conservation of the whitebreasted cormorant, *Phalacrocorax carbo*, on the southern African coast. *Gerfaut* **72:** 188–220.

Brown, R. E. & Macdonald, D. W. (1985). *Social odours in mammals* **2.** Oxford: Oxford University Press.

Cooper, J., Brooke, R. K., Shelton, P. A. & Crawford, R. J. M. (1982). Distribution, population size and conservation of the Cape cormorant *Phalacrocorax capensis*. *Fish. Bull. S. Afr.* **16:** 121–143.

Crawford, R. J. M., Shelton, P. A., Cooper, J. & Brooke, R. K. (1983). Distribution, population size and conservation of the Cape gannet *Morus capensis*. *S. Afr. J. Mar. Sci.* **1:** 153–174.

Giess, W. (1971). Vegetation map for South West Africa. *Dinteria* **4:** 1–114.

Nel, J. A. J. & Loutit, R. (1986). The diet of black-backed jackals, *Canis mesomelas*, on the Namib Desert coast. *Cimbebasia* (Ser. A) **8:** 91–96.

Odum, E. P. (1971). *Fundamentals of ecology*. Philadelphia: W. B. Saunders.

Shannon, L. V., Crawford, R. J. M. & Duffy, D. C. (1984). Pelagic fisheries and warm events: a comparative study. *S. Afr. J. Sci.* **80:** 51–60.

Shaughnessy, P. D. (1985). Interactions between fisheries and Cape fur seals in southern Africa. In *Marine mammals and fisheries*: 119–134. Beddington, J. R., Beverton, R. J. H. & Lavigne, D.M. (Eds). London: George Allen & Unwin.

Shelton, P. A., Crawford, R. J. M., Cooper, J. & Brooke, R. K. (1984). Distribution, population size and conservation of the jackass penguin *Spheniscus demersus*. *S. Afr. J. Mar. Sci.* No. 2: 217–257.

Shortridge, G. C. (1934). *The mammals of South West Africa*. London: William Heinemann Ltd.

Siegfried, W. R. (1977). Mussel-dropping behaviour of kelp gulls. *S. Afr. J. Sci.* **73:** 337–341.

Siegfried, W. R. (1984). An analysis of faecal pellets of the brown hyaena on the Namib coast. *S. Afr. J. Zool.* **19:** 61.

Skinner, J. D. & van Aarde, R. J. (1981). The distribution and ecology of the brown hyaena *Hyaena brunnea* and the spotted hyaena *Crocuta crocuta* in the central Namib Desert. *Madoqua* **12:** 231–239.

Stuart, C. T. (1976). Diet of the black-backed jackal *Canis mesomelas* in the central Namib Desert, South West Africa. *Zool. afr.* **11:** 193–205.

Stuart, C. T. & Shaugnessy, P. D. (1984). Content of *Hyaena brunnea* and *Canis mesomelas* scats from southern coastal Namibia. *Mammalia* **48:** 611–612.

Underhill, L. G. & Whitelaw, D. A. (1977). *An ornithological expedition to the Namib coast summer 1976–77.* Cape Town: Western Cape Wader Group.

I-85

F.

J. Zool., Lond. (1987) **213,** 95–106

The activity patterns of the Pyrenean desman (*Galemys pyrenaicus*) (Insectivora:Talpidae), as determined under natural conditions

R. D. STONE

Culterty Field Station, University of Aberdeen, Department of Zoology, Newburgh,
Aberdeenshire, AB4 0AA, Scotland

(*Accepted 17 February 1987*)

(With 2 plates and 3 figures in the text)

The activity patterns of free-ranging desmans (*Galemys pyrenaicus*) on three streams in the French Pyrenees were investigated. Data were obtained using an automatic radiotracking system to monitor an animal's presence at, or absence from, its nest site. Individuals displayed two distinct periods of activity during each diel period throughout this study (May–July), a short diurnal period of activity and a longer nocturnal one. The daily onset and cessation of activity for all desmans on each stream was highly synchronized. These findings are discussed with relation to prey availability and the social ecology of the species.

Contents

Introduction

Interest in the rhythms of animal behaviour derives from the recognition that the biological value of behaviour depends as much on when it occurs as on the particular form which it takes (Enright, 1970). For most animals, the environment represents a complex array of fluctuating variables and the manner by which individuals cope with such variables may be viewed as daily or seasonal strategies related to the time structure of the environment. Knowledge of the rhythms of activity would therefore contribute a great deal towards an understanding of the ecology of the species.

The activity rhythms of many small mammals may be defined in terms of two distinct behavioural rhythms: a diel (circadian) rhythm and a shorter-term one (Grodzinsky, 1963). The circadian rhythm is largely governed by external environmental variables such as changes in light intensity (Swift, 1980; Erkert, 1982), lunar periodicity (Lockard & Owings, 1974) or temperature (Bernstein, 1972). Activities governed by a circadian rhythm are often bimodal and well

Present address: Université de Lausanne, Institut de zoologie et d'écologie animale, Batiment de Biologie, 1015 Lausanne, Switzerland

0022-5460/87/009095 + 12 $03.00

synchronized on a daily basis. Species with rhythms that illustrate this include *Apodemus sylvaticus* (Elton, Ford, Baker & Gardner, 1931; Kikkawa, 1964; Gurnell, 1975; Wolton, 1983), *Peromyscus* spp. (Marten, 1973) and *Sigmodon hispidus* (Calhoun, 1945). In contrast, short-term, ultradian rhythms depend largely on metabolic demands such as hunger, thirst and defecation. The occurrence of short-term cycles of activity has also been well documented for small mammals such as shrews (*Sorex minutus* and *S. araneus*, Crowcroft, 1954 and *Crocidura russula*, Genoud & Vogel, 1981), voles (*Microtus arvalis*, Daan & Slopsema, 1978, *Clethrionomys glareolus*, Miller, 1955 and *Arvicola terrestris*, Airoldi, 1979) and moles (*Talpa europaea*, Godfrey, 1955; Woods & Mead-Briggs, 1978; Stone & Gorman, 1985; Stone, 1986). To date, however, there have been no studies which describe the activity patterns of free-ranging aquatic insectivores.

The Pyrenean desman (*Galemys pyrenaicus*) is a small, semi-aquatic talpid insectivore. An inhabitant of montane streams, this species has seldom been observed in its natural environment, where it feeds on freshwater invertebrates. Although generally considered to be a nocturnal species, this has never been proven. In this study, some aspects of the activity patterns of unrestricted radio-tagged desmans were monitored automatically in the field. Further details on social behaviour, also determined by radiotracking, are described elsewhere (Stone, 1985, 1987). The principal aim of this paper is to describe the activity patterns of desmans at three disjunct sites in the French Pyrenees and to discuss the possible influences affecting their activity and those which might account for the high level of synchrony observed. The consequences of such behaviour shall be discussed with respect to the social organization of this species. Finally, in this, the first detailed account of the desman's ecology dealing with the activity of free-living individuals, nest sites which hitherto have not been located, are also described.

Methods

This study was carried out on 3 streams (Artillac, Nédé and Bouigane) in the Ariège region of the French Pyrenees (43 N, 1 E) during June and July 1983, and May and June 1984. Details of the study sites are given in Stone, 1985 and 1986. Desmans were captured in partially-submerged, unbaited wire-mesh eel traps, which were checked every 2 hours during the night (22:00 06:00 h) to prevent casualties and to avoid the removal of animals from their territories for long periods.

Radiotracking techniques were applied to determine the social organization of populations and the activity patterns of individuals. Radiotransmitters (3 g) of a fixed frequency in the 173 MHz range were attached to 2·3 mm wide, self-locking cable ties (Radiospares Ltd.) with cyanoacrylate glue, encapsulated in fibreglass resin and attached around the narrow base of the desman's tail. All animals were retained in the traps for 10 15 min to ensure that the transmitter was fitted correctly, before being released at the capture site.

Activity patterns, as revealed by the animal's presence at, or absence from, the nest, were automatically recorded. Nests were initially located using an AVM LA-12 radio receiver (AVM Instruments Company Ltd.) fitted with a directional 3-element Yagi aerial. A miniature directional loop antenna attached to this receiver could detect the radio signal at a distance of 1m from the nest. Data were registered on a Grants Instruments (Barrington, Cambridge, UK) chart recorder (Model CBC-1) used in conjunction with this receiver. The recorder was accurate to within 5 min in each 24-h period; it was checked and reset daily if necessary. The interpretation of the printed chart record was straightforward, as there was generally a clear difference on the chart between the time when the animal was at the nest and when it was not. Some fluctuations on the chart indicated that individuals were not stationary throughout the period of time spent at the nest, but occasionally moved around within the nest chamber. *Brown's nautical almanac* (Brown, 1983, 1984) was used to determine the timing of sunrise and sunset for the Ariège region.

In this paper, data are represented in 2 ways: first, on a daily active inactive basis and, secondly, as a percentage of the time spent inactive (Fig. 1). For the latter, the number of occasions the animal was absent from its nest for more than 15 min in each 30-min interval over a 24-h period, was expressed as a percentage of the total number of days for which that animal was monitored. This percentage was plotted against respective time intervals to form histograms (Fig. 1).

When active, desmans were radiotracked to determine their movements and patterns of spatial utilization (Stone, 1986, 1987). This aspect of the study also allowed for the examination of temporary shelters which were used infrequently during the main periods of activity.

PLATE 1. A Pyrenean desman (*Galemys pyrenaicus*).

Results

A total of 38 desmans (21 males, 17 females) were captured during both study periods, of which 33 (17 males, 16 females) were fitted with transmitters. Only those for which data had been gathered for more than seven consecutive days were considered for the analysis of activity (Table 1). Thus sufficient data were obtained for only 22 animals (13 males, 9 females). Data for more than seven days could not be obtained for all animals because of transmitter failure, dispersal and occasional movements between nest sites.

PLATE II. Close up of snout of a Pyrenean desman (*Galemys pyrenaicus*).

Social organization

The social organization of the Pyrenean desman has been detailed elsewhere (Stone, 1985, 1987), but a brief summary will assist the reader. Desman populations are composed of sedentary and transient members. The sedentary animals are pairs of resident adult male and female desmans living in the same section of stream but utilizing separate nest sites. Females occupied a smaller home range ($\bar{x} = 301\text{m} \pm 7\text{m}, n = 7$) than males ($\bar{x} = 429\text{m} \pm 10\text{m}, n = 7$) ($P \leqslant 0{\cdot}001$), and their range was always contained within that of the male. The range was defended by the resident male against neighbouring conspecifics. This was achieved mainly by active patrolling and vigilance (Stone, 1985), but scent-marking is also believed to be an important factor in this process (Stone, 1986). Resident males spend most of their active time at the peripheral regions of their linear territories. Females may, however, also participate in territorial defence, their activities being concentrated within the central region of the shared territory.

The transient desmans are seasonally-dispersing juveniles and single, unpaired adults of each sex which occupy temporary ranges. Territorial defence, as practised by residents, was not apparent amongst members of this group (Stone, 1987), individuals of which also occupied a single nest site. The average home range for juveniles and solitary adults was ($\bar{x} = 249\text{m} \pm 30\text{m}, n = 4$) and

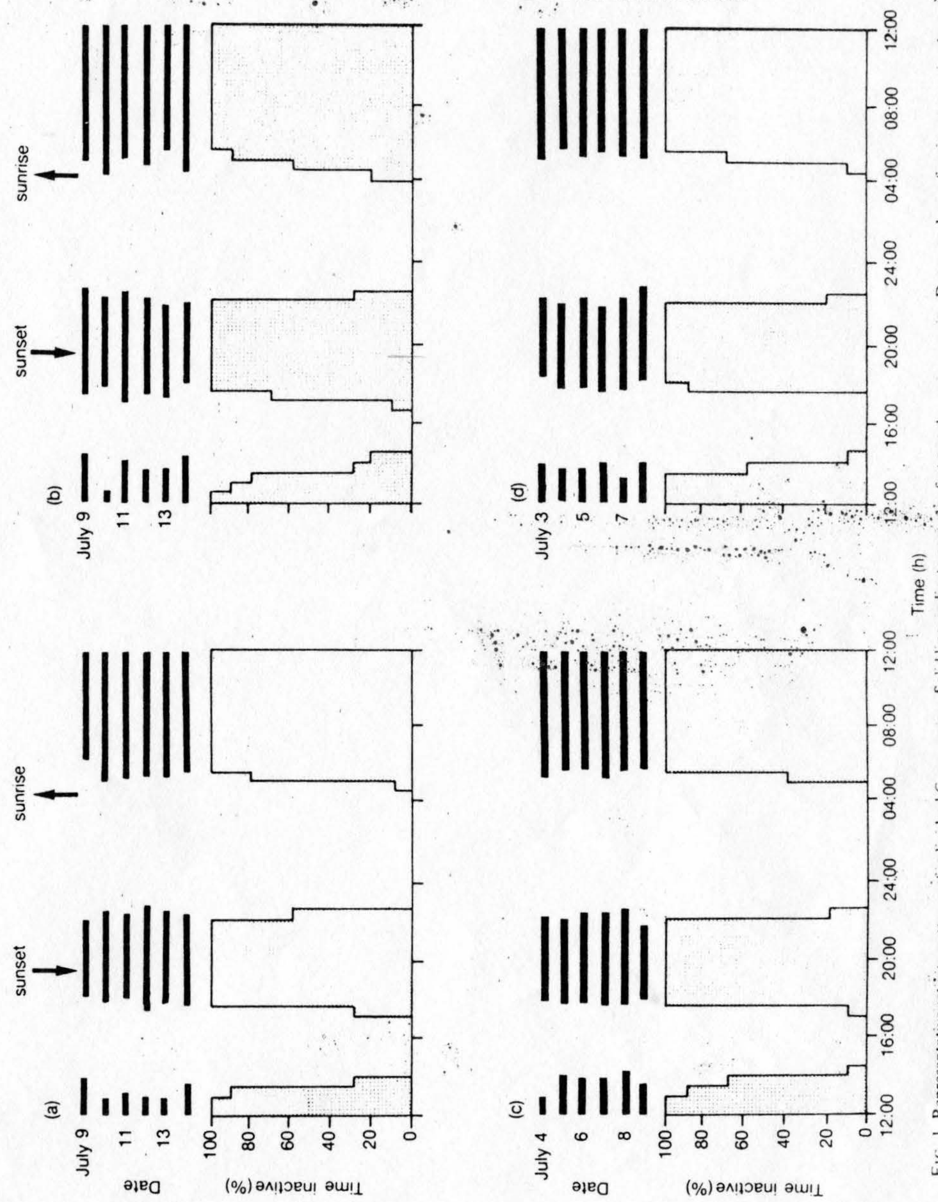

FIG. 1. Representative activity patterns of individual *G. pyrenaicus*. Solid lines indicate periods of rest at the main nest site. Data are shown for six consecutive days for a paired adult male (a), a paired adult female (b), a juvenile male (c) and a single adult female (d). In reality, at least 7 days of continuous monitoring were obtained for each animal. Shaded areas beneath the histograms represent the percentage of time spent at the nest for the duration of the period of tracking.

TABLE I

Schedule of radiotracking dates at each study area during 1983 and 1984, showing the relative amount of time spent active throughout the study period by individual desmans

↑	Desman	Status	Weight (g)	Dates of radio-tracking	Tracking site	Mean day-length (h)	Mean total time active (h)	Daytime active (%)	Night-time active (%)
(13)	M 1	Adult	58	13 June 1983 25 June 1983	Nédé	15′26″	11′48″	28	72
(21)	M 2	Adult	59	09 June 1983 29 June 1983	Artillac	15′26″	11′20″	30	70
(21)	M 3	Adult	59	27 June 1983 18 July 1983	Artillac	15′26″	11′42″	25	75
→ (23)	M 4	Adult	62	26 June 1983 19 July 1983	Artillac	15′26″	11′12″	29	71
(13)	M 5	Juvenile	40	02 July 1983 14 July 1983	Artillac	15′26″	10′54″	29	71
(15)	M 6	Adult	69	04 July 1983 18 July 1983	Artillac	15′26″	11′00″	30	70
(13)	M 7	Adult	59	02 June 1984 14 June 1984	Bouigane	15′35″	10′42″	22	78
(10)	M 8	Adult	62	05 June 1984 14 June 1984	Bouigane	15′35″	11′24″	23	77
(14)	M 9	Adult	59	07 June 1984 20 June 1984	Bouigane	15′35″	12′00″	17	83
(10)	M 10	Adult	58	04 June 1984 13 June 1984	Bouigane	15′35″	10′36″	21	79
(12)	M 11	Juvenile	35	04 June 1984 15 June 1984	Bouigane	15′35″	11′24″	16	84
(11)	M 12	Juvenile	37	04 June 1984 14 June 1984	Bouigane	15′35″	11′48″	11	89
(11)	M 13	Adult	65	21 May 1984 31 May 1984	Artillac	15′35″	10′48″	21	79
(9)	F 1	Juvenile	45	14 June 1983 22 June 1983	Nédé	15′26″	11′40″	27	73
(7)	F 2	Adult	54	16 June 1983 22 June 1983	Nédé	15′26″	11′00″	25	75
(8)	F 3	Adult	59	24 June 1983 02 July 1983	Nédé	15′26″	10′18″	28	72
(21)	F 4	Adult	58	09 July 1983 29 July 1983	Artillac	15′26″	12′00″	28	72
(13)	F 5	Adult	55	03 July 1983 15 July 1983	Artillac	15′26″	11′06″	29	71
(16)	F 6	Adult	58	03 July 1983 18 July 1983	Artillac	15′26″	12′00″	25	75
(13)	F 7	Adult	56	05 June 1984 17 June 1984	Bouigane	15′35″	10′30″	20	80
(14)	F 8	Adult	56	06 June 1984 19 June 1984	Bouigane	15′35″	10′48″	16	84
(14)	F 9	Adult	58	07 June 1984 20 June 1984	Bouigane	15′35″	12′00″	22	78

($\bar{x} = 572\text{m} \pm 193\text{m}$, $n = 3$), respectively ($P \leq 0{\cdot}001$). Transient desmans did not always display site fidelity, in contrast to sedentary paired adults, and were recorded on occasion as passing through the ranges of resident animals (Stone, 1987).

The nest site

Desmans maintain two shelters, one a temporary shelter, used irregularly, for brief (10–15 min) periods of rest, the other a main nest site for longer periods. In general, only one principal nest site was used exclusively by each animal. Temporary shelters were located in small crevices in the banks of the stream and in heaps of rocks along its course: no nesting material was found at those. Unlike most other members of this family, the Pyrenean desman does not show any adaptations to a fossorial existence, though the long, sharp claws on the forefeet may play a role in enlarging existing underground chambers. Thus, the shelters used are generally naturally occurring crevices between rocks in stone walls, or along the roots of trees. There are no outwardly visible signs of the shelters from the surface.

Desmans restrict their movements to a stream (Stone, 1986) and nest sites are located along its banks. Excavated nest sites reveal that the entrances are always submerged and sloping upwards and away from the stream. Nest sites are simple in structure with a single passage leading to a circular nest chamber located up to 1m away from the stream. The chamber (mean diameter 15 cm) usually contains small twigs, leaves and grasses which are woven into a sphere, similar to the nest of the European mole (*Talpa europaea*) (Stone, pers. obs.). Niethammer (1970) observed that captive desmans usually carry such material in the mouth.

Activity patterns

The data from the present study show that desmans have a distinct daily pattern of activity (Fig. 1). Although primarily a nocturnal species, a secondary afternoon period of activity was also evident. This was seen amongst all animals in each of the social groups: juveniles, solitary and paired sedentary adults (Fig. 1). Both male and female desmans alike were more active in darkness than during daylight hours (Table I).

Variations in the timing of activity were observed both between the two study periods and between individuals on different streams (Figs 2 and 3). The actual duration of activity for individuals on different streams did not, however, vary significantly. Simultaneous radiotracking of individuals (Stone, 1986) has shown that, within each 24-h period, each animal spent approximately 53% of its time at the nest site, 45% actively feeding and moving along the stream, and 2% resting in crevices outside its main nest. When tracking active animals, it was not possible to distinguish between certain activities such as diving, feeding or swimming. Therefore, each of these activities has been included in the general value for movement. Feeding by both sexes was, however, thought to be more intensive during the nocturnal period of activity than during the afternoon, when animals were only rarely seen diving.

The activity cycles of individual desmans of both sexes and of different social status, within a given area, were closely synchronized on a daily basis (Fig. 1) and there was little variation in the timing of onset or cessation of activity between individuals. Any such instances were accounted for by adverse weather conditions (see later). During June and July 1983, all desmans on both the Artillac and Nédé streams became active shortly after 22:00 h and remained so until 04:30–05:00 h (Fig. 2), with brief (10–15 min), intermittent rest periods at irregular intervals along the stream. Desmans remained inactive throughout the morning and resumed activity around 14:00 for a period of 3–4 h.

During May and June 1984, the activity of individual desmans on the Bouigane stream was again synchronized; the daylight active phase began at 11:45–12:00 h, and the animals remained

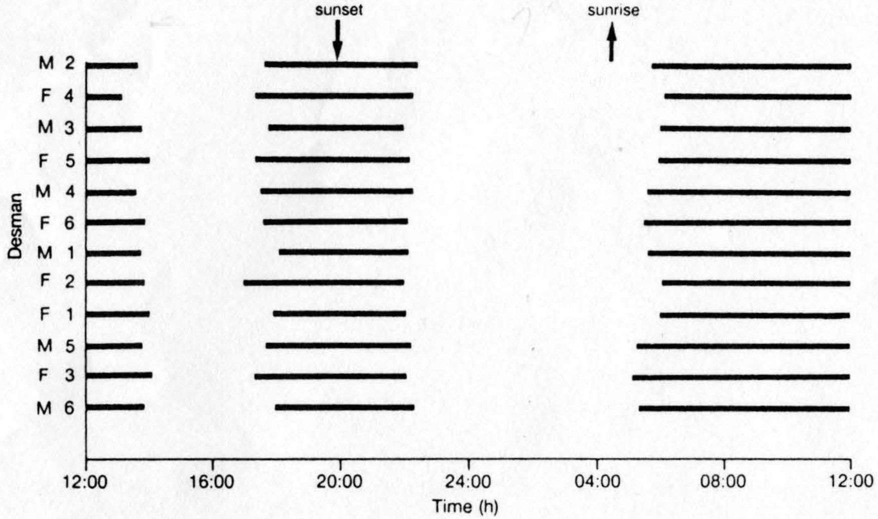

FIG. 2. The activity patterns of male (M) and female (F) desmans which were radiotracked on the Artillac and Nédé streams during June and July 1983. Solid lines indicate the mean period of inactivity (time spent at the nest) for the duration of study.

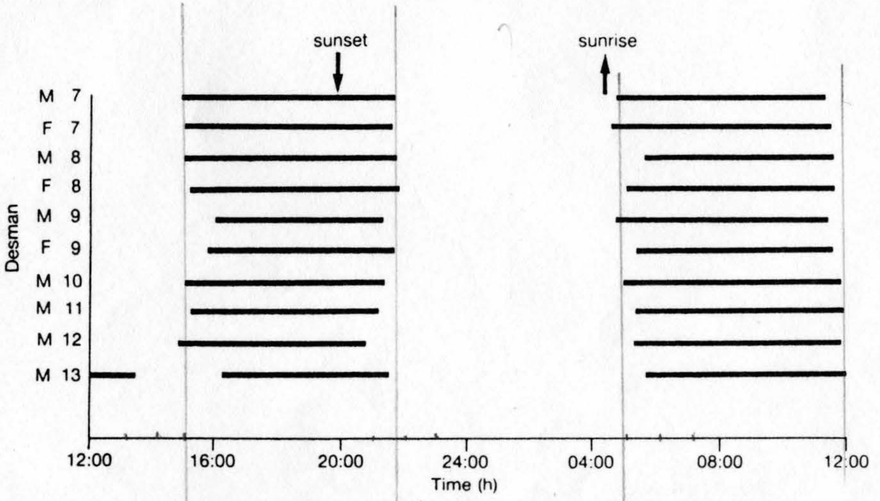

FIG. 3. The activity patterns of male (M) and female (F) desmans which were radiotracked on the Artillac and Bouigane streams during May and June 1984. Details as in Fig. 2

active for a period of 3 - 4 h (Fig. 3). The later, evening period of activity was similar in duration and timing to that observed during 1983 on the Artillac and Nédé streams. In 1984, only one male (male 13) was successfully tracked on the Artillac stream and its pattern of activity differed from those desmans tracked on the Bouigane during that year, but was similar to those tracked on the Artillac during 1983.

Both temperature and rainfall influenced the behaviour and activity of desmans. Thunderstorms, accompanied by rainfall, delayed the emergence of desmans by several hours. On two separate occasions, marked desmans returned to the nest after only 90 min of activity; on both occasions probably due to the onset of heavy rainfall. All individuals emerged later the same night, when conditions improved.

Discussion

Research on the activity patterns of small mammals under natural conditions has been limited in its scope by difficulties in observing or following the study animal. Activity patterns recorded under laboratory or captive conditions have been the main and, in many cases, exclusive source of information concerning biological rhythms. However, the controlled conditions that permit observations of these aspects of rhythmicity necessarily preclude observations on the influence of many environmental factors that are major determinants of activity patterns in the field (Kavanau, 1969; Ashby 1972). In general, it is unwise to extrapolate results, obtained under laboratory conditions, to a field situation, in view of the controlled conditions of the former and the variable, unpredictable conditions of the latter. Many examples illustrating this effect are now available, e.g. Genoud & Vogel (1981) who, in comparing the activity of *Crocidura russula* both in captivity and in a natural situation (the latter determined by radioisotope tracking), concluded that their 'observations made in captivity, even under climatic conditions approaching those in the field, can in no case be extended to free-living animals'.

Radiotracking is particularly well suited to the task of monitoring an animal's presence at, or absence from, its nest for extensive periods of time. It is advantageous over other techniques as it provides a means of continuous monitoring without causing undue stress or interference to the animal. In addition, it is preferable to techniques such as radioisotope tracking, as many individuals may be monitored simultaneously—rarely possible with the latter technique. Finally, such results are more readily accessible to biological interpretation than those carried out on restricted, captive species, as the animals are free-ranging in their natural environment.

The present data suggest that the basic temporal pattern of activity in *Galemys*, at least during the summer months, is a short-term rhythm in the form of a distinct biphasic daily pattern. Additional brief periods of rest are taken at irregular intervals along the length of the stream without recourse to the main nest site. A recent report (Richard, 1985) dealing only with the activity of captive male desmans, suggests a far more irregular, polyphasic pattern of activity. In this latter study, however, activity was taken as a measure of the number of times the captive animal interrupted a light beam as it passed between the nest and feeding area. The provision of food and the proximity of the nest chamber, to which the captive animals often returned to eat and cache food (Stone, pers. obs.), are additional factors likely to have influenced the timing and duration of the activity periods of these captive animals.

What, therefore, are the functional advantages of this pattern of behaviour?

One of the adaptive functions of short-term rhythms is the synchronization of periods of activity among members of a population (Stebbins, 1984). This phenomenon of social synchronization has been well documented in studies of circadian rhythms (Weigent, 1961; Kikkawa, 1964; Ambrose, 1973; Stebbins, 1974; Madison, 1978), but less frequently amongst those of short-term rhythms (Daan & Slopsema, 1978). Possible benefits which accrue from such behaviour include reduced levels of predation (Daan & Slopsema, 1978), increased efficiency in feeding (Lehmann, 1976), and mutual avoidance of conspecifics (Stone, 1986). According to the present data, within each particular stream, the onset and cessation of activity amongst neighbouring desmans was highly synchronized and the overall biphasic pattern was upheld by all members of each population studied. Avoidance of predators is unlikely to be the key factor accounting for the observed activity patterns in desmans, since being active during both day and night they are subject to a wide range of potential predators. Yet, social synchronization may play an integral role in reducing the level of predation, since the risk of an individual being killed, if active at the same time as its conspecifics, might be less than if it was active independently of its conspecifics.

The mutual avoidance of neighbouring conspecifics may be facilitated through a system of social synchronization. This may be achieved either through the regulation of activity patterns, e.g. *Talpa europaea* (Stone, 1986), or movement patterns, e.g. *Tamias striatus* (Getty, 1981). In *Galemys*, the utilization of areas of range overlap by both neighbours during different periods of daily activity (Stone, 1987) allows for their mutual avoidance. This, in turn, reduces the likelihood of aggressive encounters as neighbouring animals rarely come into direct contact. Indirect communication is, however, possible via the regular deposition of scent marks along the boundaries of individual territories (Stone, 1986).

A final advantage of social synchronization may relate to diet and to being active at a time when prey availability is at its highest. This has often been shown to be the case. For example, some species, such as *Apodemus sylvaticus* and *Peromyscus maniculatus*, feed almost exclusively on seeds and arthropods (Watts, 1968), which are high in protein and fat. The high calorific value of such a diet obviates the need for repetitive short-term feeding bouts and both of these species generally exhibit a bimodal pattern of activity. In contrast, herbivorous species such as *Clethrionomys glareolus*, rely on intestinal bacteria to break down the cell walls of plants and require a high intake of bulky, low-value food at regular intervals throughout the 24 h. These species, however, feed mainly on immobile prey. Insectivores, in contrast, feed on highly mobile invertebrates and vary considerably in their pattern of activity; many species of shrew have polyphasic patterns of activity (Crowcroft, 1954; Genoud & Vogel, 1981; Vogel, Genoud & Frey, 1981), which allow for frequent foraging bouts, whereas larger species, such as the European hedgehog (*Erinaceus europaeus*), and the common tenrec (*Tenrec ecaudatus*), are largely nocturnal and have just one extended period of activity (Reeve, 1982; Nicoll, 1982, respectively).

It is well known that many stream invertebrates increase their activity following sunset, when they rise up into the water current and may be deposited downstream, in the phenomenon known as stream drift (Waters, 1962, 1965). Thus, at such times, prey would be more readily available to foraging animals. In addition, within this nocturnal period, many aquatic insect larvae, as well as their aerial counterparts, display a strong biphasic periodicity in their activity, which is characterized by post-sunset and pre-dawn peaks of activity. Racey & Swift (1985) have demonstrated that the attempted feeding rates of pipistrelle bats (*Pipistrellus pipistrellus*) are closely correlated with this diel abundance of aerial prey. At a certain, critical time when insect activity is reduced, bats cease to feed and await the secondary surge of insects in the pre-dawn period. In the present study, the temporal abundance of prey was reflected by the foraging and feeding behaviour of desmans, which was always concentrated within this period of darkness. Unfortunately, it was not possible to determine whether the feeding success of individuals varied according to the temporal availability of prey. Desmans, although active for a shorter period during daylight, were rarely observed feeding during this time.

The existence of such clear-cut rhythms in the daily activity patterns of desmans under natural conditions and, to a certain extent, the degree of synchrony of these rhythms among members of a population within the same region, suggest that desmans perceive external cues which initiate or terminate activity. From the present data, sunrise appears to be the most likely cue terminating activity, as all individuals returned to their respective nest sites within 30 min of sunrise (Figs 2 and 3).

Since the present data were obtained during a limited period of the year, they cannot represent all possible variations in the desman's activity throughout the year but do, nevertheless, serve to illustrate two important features which can only be realised from this type of study. First, they allow the animals' movements and behavioural patterns to be related with the timing of activity, thus contributing to a better understanding of the species' ecology and, secondly, they show the extent of social synchronization in this species, an important feature which could not be realised in a captive situation.

This study was made possible by the financial support of The Nuffield Foundation, The Carnegie Trust for the Universities of Scotland, the British Ecological Society and the University of Aberdeen. I gratefully acknowledge the support of each of these organizations. I am also indebted to Profs P. Vogel and P. A. Racey, Drs M. L. Gorman and M. Genoud, for their valuable criticism and discussions on this manuscript. In addition, comments from a referee have greatly improved the final version of this paper. Mr J. A. Morris (I.T.E. Banchory) kindly allowed me to use his design of radiotransmitter and provided excellent guidance during its construction. Dr C. Juberthie kindly made facilities available to me during my stay at C.N.R.S. at Moulis and Dr P. B. Richard greatly assisted in the preliminary stages of the study. Prof. P. Vogel, Drs H. Richner and G. J. Pierce were willing assistants with field work and I gratefully acknowledge their help. Finally, my sincere thanks to Olga Sheean-Stone for her undaunting support throughout this study.

REFERENCES

Airoldi, J.-P. (1979). Etude du rythme d'activité du campagnol terrestre, *Arvicola terrestris sherman* Shaw (Mammalia, Rodentia). *Mammalia* **43:** 25–52.

Ambrose, H. (1973). An experimental study of some factors affecting the spatial and temporal activity of *Microtus pennsylvanicus*. *J. Mammal.* **54:** 79–110.

Ashby, K. R. (1972). Patterns of daily activity in mammals. *Mamm. Rev.* **1:** 171–185.

Bernstein, I. S. (1972). Daily activity cycles and weather influences on a pigtail monkey group. *Folia primatol.* **18:** 390–415.

Brown, T. N. (1983). *Brown's nautical almanac*. Brown, T. N. (Ed.). Glasgow: Brown, Son & Ferguson Ltd.

Brown, T. N. (1984). *Brown's nautical almanac*. Brown, T. N. (Ed.). Glasgow: Brown, Son & Ferguson Ltd.

Calhoun, J. B. (1945). Diel activity rhythms of the rodents *Microtus ochrogaster* and *Sigmodon hispidus hispidus*. *Ecology* **26:** 251–273.

Crowcroft, W. P. (1954). The daily cycle of activity in British shrews. *Proc. zool. Soc. Lond.* **123:** 715–729.

Daan, S. & Slopsema, S. (1978). Short-term rhythms in foraging behaviour of the common vole, *Microtus arvalis*. *J. comp Physiol.* **127:** 215–227.

Elton, C., Ford, E. B., Baker, J. R. & Gardner, A. D. (1931). The health and parasites of a wild mouse population. *Proc. zool. Soc. Lond.* **1931:** 657–721.

Enright, J. (1970). Ecological aspects of endogenous rhythmicity. *A. Rev. Ecol. Syst.* **3:** 1–32.

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

Genoud, M. & Vogel, P. (1981). The activity of *Crocidura russula* (Insectivora; Soricidae) in the field and in captivity. *Z. Saugetierk.* **46:** 222–232.

Getty, T. (1981). Territorial behaviour of eastern chipmunks (*Tamias striatus*): encounter avoidance and spatial time-sharing. *Ecology* **62:** 915–921.

Godfrey, G. K. (1955). A field study of the activity of the mole (*Talpa europaea*). *Ecology* **36:** 678–685.

Grodzinsky, W. (1963). Seasonal changes in the circadian activity of small rodents. *Ecol. Pol.* (*B*) **9:** 3–17.

Gurnell, J. (1975). Notes on the activity of wild Wood mice, *Apodemus sylvaticus*, in artificial enclosures. *J. Zool., Lond.* **175:** 219–229.

Kavanau, J. L. (1969). Influences of light on activity of small mammals. *Ecology* **50:** 548–557.

Kikkawa, J. (1964). Movement, activity and distribution of the small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus* in woodland. *J. Anim. Ecol.* **33:** 259–299.

Lehmann, V. (1976). Short-term and circadian rhythms in the behaviour of the vole, *Microtus agrestis* (L.). *Oecologia* **23:** 185–199.

Lockard, R. B. & Owings, D. H. (1974). Non-related surface activity of bannertail (*Dipodomys spectabilis*) and fresno (*D. nitratoides*) kangaroo rats. *Anim. Behav.* **22:** 262–273.

Madison, D. (1978). Movement indicators of reproductive events among female meadow voles as revealed by radiotelemetry. *J. Mammal.* **59:** 835–843.

Marten, G. G. (1973). Time patterns of *Peromyscus* activity and their correlation with weather. *J. Mammal.* **54:** 169–188.

Miller, R. S. (1955). Activity rhythms in the Wood mouse (*Apodemus sylvaticus*) and the Bank vole (*Clethrionomys glareolus*). *Proc. zool. Soc. Lond.* **125:** 505–519.

Nicoll, M. E. (1982). *Reproductive ecology of* ***Tenrec ecaudatus*** *(Insectivora: Tenrecidae) in the Seychelles.* Unpubl. PhD thesis, University of Aberdeen.

Niethammer, G. (1970). Beobachtungen am Pyrenean-Desman, *Galemys pyrenaica*. *Bonn. zool. Beitr.* **21:** 157–182.

Racey, P. A. & Swift, S. M. (1985). Feeding ecology of *Pipistrellus pipistrellus* (Schreber) (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. *J. Anim. Ecol.* **54:** 205–215.

Reeve, N. J. (1982). The home range of the hedgehog as revealed by a radio tracking study. *Symp. zool. Soc. Lond.* No. 49: 207–230.

Richard, P. B. (1985). Etude préliminaire sur les rythmes d'activité du desman (*Galemys pyrenaicus*) en captivité (Insectivores, Talpidés). *Mammalia* **49:** 317–323.

Stebbins, L. L. (1974). Response of circadian rhythms in *Clethrionomys* mice to a transfer from 60° N to 53° N. *Oikos* **25:** 108–113.

Stebbins, L. L. (1984). Over-wintering activity of *Peromyscus maniculatus*, *Clethrionomys gapperi*, *C. rutilus*, *Eutamias amoenus* and *Microtus pennsylvanicus*. *Spec. Publs Carnegie Mus. nat. Hist.* **10:** 301–315.

Stone, R. D. (1985). Home range movements of the Pyrenean desman (*Galemys pyrenaicus*) (Insectivora: Talpidae). *Z. angew. Zool.* **72:** 25–37.

Stone, R. D. (1986). *The social ecology of the European mole (* **Talpa europaea** *L.) and the Pyrenean desman* (**Galemys pyrenaicus** G.). Unpubl. PhD thesis, University of Aberdeen.

Stone, R. D. (1987). The social ecology of the Pyrenean desman (*Galemys pyrenaicus*) (Insectivora: Talpidae), as revealed by radiotelemetry. *J. Zool., Lond.* **212:** 117–129.

Stone, R. D. & Gorman, M. L. (1985). Social organisation of the European mole (*Talpa europaea*) and the Pyrenean desman (*Galemys pyrenaicus*). *Mamm. Rev.* **15:** 35–42.

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

Vogel, P., Genoud, M. & Frey, H. (1981). Rythme journalier d'activité chez quelques Crocidurinae africains et européens (Soricidae, Insectivora). *Terre Vie* **35:** 97–108.

Waters, T. F. (1962). Diurnal periodicity in the drift of stream invertebrates. *Ecology* **43:** 316–320.

Waters, T. F. (1965). Interpretation of invertebrate drift in streams. *Ecology* **46:** 327–334.

Watts, C. H. S. (1968). The foods eaten by wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) in Wytham Woods, Berkshire. *J. Anim. Ecol.* **37:** 25–41.

Weigent, R. (1961). Respiratory energy loss and activity patterns in the meadow vole, *Microtus pennsylvanicus*. *Ecology* **42:** 245–253.

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

Woods, J. A. & Mead-Briggs, A. R. (1978). The daily cycle of activity in the mole (*Talpa europaea*) and its seasonal changes, as revealed by radioactive monitoring of the nest. *J. Zool., Lond.* **184:** 563–572.

J. Zool., Lond. (1987) **213**, 107–115

Estimates of forces exerted by the jaw muscles of some reptiles

ALICE G. SINCLAIR & R. McN. ALEXANDER

Department of Pure and Applied Zoology, University of Leeds, Leeds LS2 9JT

(*Accepted 17 February 1987*)

(With 3 figures in the text)

Masses and muscle fibre lengths have been determined for the jaw muscles of *Chrysemys* (Chelonia), *Varanus* (Lacertilia) and *Caiman* (Crocodilia). Hence the force that each muscle can exert has been estimated. The position and direction of the line of action of each force have also been determined. The results are used to calculate the magnitude and direction of the bite forces that each reptile could exert, at particular positions in its mouth, and the magnitude and direction of the reactions at the jaw articulation.

Contents

Introduction

The various jaw-closing muscles of reptiles pull in different directions: some pull dorsally and posteriorly, and others dorsally and anteriorly (Fig. 1a). The adductor mandibulae externus (which pulls dorsally and posteriorly) is the largest jaw muscle in most reptiles, but the pterygoideus (which pulls dorsally and anteriorly) is the largest in crocodilians (Schumacher, 1973). What is the significance of the different directions of pull, and of the relative sizes of the various muscles? J. M. Smith & Savage (1959) showed for mammals how different directions of pull could reduce forces at the jaw articulation, and Crompton (1963) discussed the evolution of the mammalian arrangement, but there has been little discussion of jaw muscle directions in modern reptiles.

K. K. Smith (1982) made a suggestion about lizards, which have a movable quadrate-squamosal joint as well as a movable quadrate-mandibular joint. The line of action of adductor mandibulae externus runs closer to the former joint than to the latter. For the pterygoideus, the reverse is true. Consequently, the moments about both joints can be balanced simultaneously (as required for equilibrium) when both muscle groups are active. She suggested a combination of muscle forces that would achieve this when a vertical bite force acted on the posterior part of the tooth row.

We have now measured the dimensions of the jaw muscles of some reptiles and have used them to estimate the forces that the muscles could have exerted in life.

0022-5460/87/009107 + 09 $03.00