Acta Theriologica 46 (3): 295–304, 2001.
PL ISSN 0001–7051

Seasonal and sexual variation in diel activity rhythms of pine marten *Martes martes* in the Białowieża National Park (Poland)

Andrzej ZALEWSKI

Zalewski A. 2001. Seasonal and sexual variation in diel activity rhythms of pine marten *Martes martes* in the Białowieża National Park (Poland). Acta Theriologica 46: 295–304.

From 1991–1996, the activity rhythms of 14 radio-collared pine martens *Martes martes* (Linnaeus, 1758) (6 males and 8 females) were studied in the pristine deciduous and mixed forests of the Białowieża National Park. Tracking data (5823 h) indicated that the activity rhythms of pine martens varied between sexes and seasons. In spring, male activity peaked at 20.00–00.00 h, whereas in summer and autumn–winter, activity was bimodal, peaking at 18.00–22.00 h and 02.00–04.00 h. Female activity in spring was more evenly distributed than that of males, but in summer their activity peaked at 20.00–00.00 h, while in autumn–winter females had a bimodal rhythm with peaks at 18.00–20.00 h and 02.00–06.00 h. In breeding females, activity rhythms changed in the course of pregnancy and nursing. On average, martens started their activity 73±209 (SD) min before sunset and finished 87 ± 245 min after sunrise. Females became active earlier than males but both sexes terminated activity at the same time. For both males and females the daily activity rhythm was not related to the diurnal course of temperature.

Mammal Research Institute, Polish Academy of Sciences, 17-230 Białowieża, Poland, e-mail: zalewski@bison.zbs.bialowieza.pl

Key words: *Martes martes*, activity rhythms, thermal stress, Białowieża National Park

Introduction

Animals adapt their circadian activity to diurnal variation in their environment, food availability, predation risk, and reproduction constraints (Aschoff 1964, Daan and Aschoff 1982). Each of these factors plays a different role relative to season but two factors have often been used as an explanation of predator's activity rhythms: predator-prey synchronisation and predation risk. It is assumed that increased predator-prey synchronisation of activity leads to increased predator hunting success. Many studies focus on this factor as an explanation of predators activity rhythms (Ables 1969, Gerell 1969, Schuh *et al*. 1971, Curio 1976, Koop and Velimirov 1982, Zielinski *et al*. 1983, Ferguson *et al*. 1988, Lodé 1995, Lariviere and Messier 1997). The pine marten *Martes martes* (Linnaeus, 1758) prey mainly on small rodents but the composition of their diet changes between seasons (Grakov 1981, Jędrzejewski *et al*. 1993). In Białowieża National Park, bank voles *Clethrio-*

nomys glareolus are the preferred prey species throughout the year and constitute, on average, 32% of the biomass consumed by martens (Jędrzejewski *et al*. 1993). Avoidance of predation by small and medium-sized predators themselves has also been suggested as the only adequate explanation of patterns of activity (Geffen and Macdonald 1993, Drew and Bissonette 1997). The pine marten is a medium-sized mustelid and could be killed by many predators and raptors (Korpimäki and Norrdahl 1989, Lindström *et al*. 1995, Okarma *et al*. 1997).

Seasonal variation of activity patterns, however, was strongly affected by variation of weather and reproduction constrains. Since the pine marten has a thin, elongated body conductive to rapid heat loss (Iversen 1972), its activity rhythm may be influenced by variation in diel temperature. At low temperature martens curtailed their activity, however, they were mostly active at night (Zalewski 2000). In winter, the American marten *Martes americana* was active during daylight hours when temperature was higher than during the night (Thompson and Colgan 1991). Male pine martens are 33% larger than females. As a consequence females need to reduce their activity during periods of cooler temperature much more than males. In winter, the smaller females need to be active more often due to higher possibility of starvation but they are active for a shorter duration (Zalewski 2000). It could be expected that females would be active more evenly in the day.

The different investment in parental care by males and females can also affect activity, and sexual differences in activity pattern are likely to occur, especially in spring and summer. At this time females invest their energy in parental care in order to maximise breeding success. In spring, females leave their cubs for short periods, but duration of activity did not differ from that in males (Zalewski 2000). Thus female activity is more evenly distributed during the day, which make them more active in daylight hours. This could result in females running a higher predation risk by raptors.

In this paper, I examine circadian rhythms of pine marten activity over a five--year period in the last remnant of pristine deciduous and mixed forests in the European lowlands, where the pine martens exist amongst very rich communities of prey and other predators (Jędrzejewska and Jędrzejewski 1998). The area has not been exploited for timber and the level of human penetration is very low. Therefore, human impact on marten behaviour is negligible. In this paper, I analysed: (1) seasonal variation in activity rhythms of pine marten; (2) differences in the daily activity rhythms between male and female; (3) variation of females activity rhythms in pregnancy and nursing.

Study area

The study was conducted in an area of north-east Poland (52°43'N, 23°54'E) within the strict reserve of Białowieża National Park (47.5 km^2 – BNP). The Park is part of a large primeval woodland covering over 1250 km^2, in which old-growth forest areas are dominated by oak-lime-hornbeam stands (44.4% of area) comprising hornbeam *Carpinus betulus*, oak *Quercus robur* and lime *Tilia cordata*, as well as scattered spruce *Picea abies*. Two other main forest types are mixed coniferous (dominated by

spruce and pine *Pinus silvestris*) and ash-alder (dominated by black alder *Alnus glutinosa* and ash *Fraxinus excelsior*). More detailed information on the vegetation of BNP is given by Faliński (1986). Old-growth forests of BNP are characterised by various age of trees (mean age of tree stands is 130 years), the presence of snags and downed logs of large diameter, and small gaps in the canopy. Human penetration (mainly pedestrian tourists) of the National Park is very low and only occurs in the south-western part of the study area.

The climate is transitional between continental and Atlantic types but continental features prevail (Olszewski 1986). During the study (1991–1996), January or February were the coldest months, with average monthly temperature reaching as low as –8.5°C, and a maximum snow cover of 63 cm. The warmest month was July, with average monthly temperature reaching a high of 22.5°C. More detailed information about the area as well as maps of the terrain are given by Jędrzejewska and Jędrzejewski (1998).

Material and methods

From 1991 to 1996, 6 male and 8 female pine martens were captured in box traps and equipped with radio-collars (AVM or Lotek; 12–25 g). Martens were located at least once daily and on some days they were monitored continuously for a time span of 4–24 h. During such continuous radiotracking, locations were taken at 15-min intervals. Marten behaviour was categorised as active (frequently switching pulse amplitude) or inactive (pulse amplitude unchanging). Since slight movements of the animal in a resting site could have been confused with true locomotor activity, the activity was recorded as occurring in the resting site if the marten's spatial position did not change despite a slight variation in the signal. In total, 23 294 activity fixes (5823 h) were recorded (15 203 for males and 8091 for females). For analysis of the diel activity rhythms in each season, the total number of fixes during 2-hour periods were taken as 100 so active fixes were thus calculated as percentages. Pooled data from three seasons: spring (16 March – 15 June), summer (16 June – 15 October) and autumn–winter (16 October – 15 March) were analysed. The first date upon which natal dens were located was accepted as parturition date, although such estimates may be 2–4 days after the actual birth.

Circadian rhythms of marten activity were also correlated with diel course of ambient temperature measured in 1960, in oak-lime hornbeam forest of BNP at 0.2 m above ground (Olszewski 1986). In 1960, average temperature in January (–4.5°C) was within the range of mean January temperatures in my study period (–0.9 to –8.5°C). The mean daily snow cover in 1960 was 6.2 cm, again within the range recorded in 1991–1996 (1.7 to 20.7 cm).

Results

Diel distribution of martens activity was not homogenous. Generally, activity levels were higher between 18.00–06.00 h followed by a decline during daylight hours (Fig. 1). In both sexes activity varied significantly between seasons (G-test for homogeneity of percentages: males – G from 25.5 to 38.0, $p < 0.01$, df = 11; females – G from 49.3 to 69.5, $p < 0.001$, df = 11). In spring, male activity peaked at 20.00–00.00 h (91 and 87% of active fixes) and was at its lowest at 08.00–14.00 h (9–10%, Fig. 1). In summer, males displayed a bimodal activity rhythm with peaks at 18.00–22.00 h (75 and 77% of active fixes) and 02.00–04.00 h (79% of active fixes; Fig. 1). Daylight activity (minimum 10% between 12.00–14.00 h) was noticeably higher in summer than during any other season. In autumn–winter, male martens also displayed a bimodal rhythm of activity with a maximum of 50–60% of active fixes.

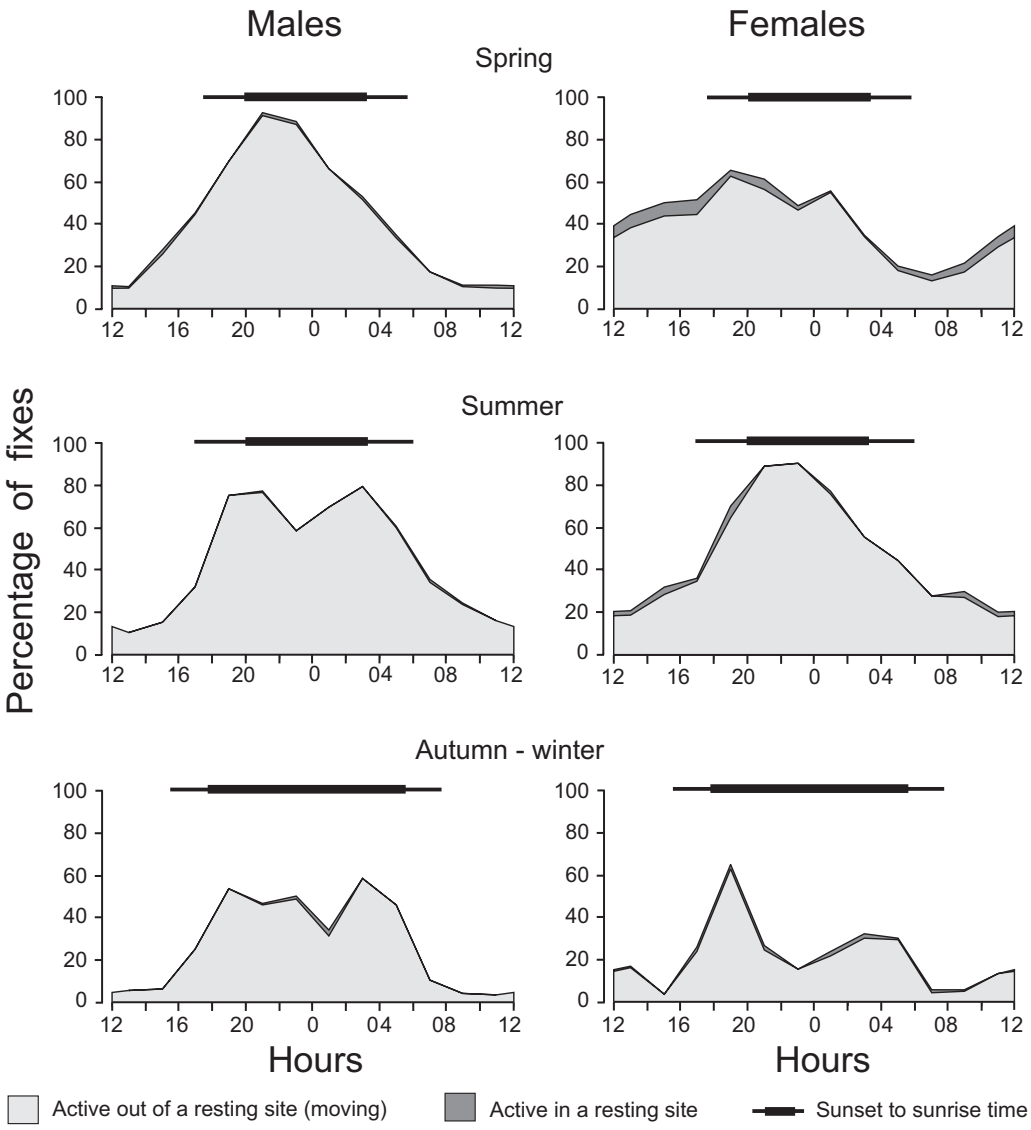

Fig. 1. Circadian activity rhythms of male (n = 6) and female (n = 8) pine martens *Martes martes* during spring (15 March–15 June), summer (16 June–15 October) and autumn–winter (16 October–15 March) in the Białowieża National Park (Poland) in 1991–1996. For each 2-hour period fixes when martens were found active were calculated as percentage of all fixes taken at 15-min intervals. Total n fixes in 2-h periods varied from 83 to 1741. Dark horizontal bars indicate the shortest and the longest time from sunset to sunrise in each season.

In spring, female activity rhythms were more evenly distributed than those of males. Their level of activity shown for 2-hour periods varied from 29% to 63%, except between 04.00–10.00 h, when it was lower (13–18%, Fig. 1). In summer, female activity peaked between 20.00–00.00 h (89–91% of active fixes). In autumn––winter, females, like males, had a bimodal activity rhythm, exhibiting a bigeminus pattern (Aschoff 1966) with the first peak markedly higher than the second.

These data show different rhythms of activity in males and females, especially in spring (spring: $G = 62.4$, $p < 0.001$; summer: $G = 22.3$, $p < 0.05$; autumn–winter: $G = 42.4$, $p < 0.05$, df = 11 in each case). In spring, females were more active than males between 10.00–16.00 h (G from 4.5 to 17.9, $p < 0.05$, df = 1) but males were significantly more active between 20.00–00.00 h ($G = 8.2$ and 12.5, $p < 0.01$, df = 1; Fig 1). In summer, the activity rhythms of the sexes were closer than at any other season but there were still significant differences between 22.00–00.00 h ($G = 6.9$, $p < 0.01$, df = 1) and 02.00–04.00 h ($G = 4.0$, $p < 0.05$, df = 1). During autumn– –winter, females decreased their activity to a much greater extent than males between 20.00–00.00 h ($G = 6.6$ and 18.6, $p < 0.05$, df = 1) and 02.00–04.00 h ($G = 6.3$, $p < 0.05$, df = 1) but were more active between 10.00–14.00 ($G = 6.3$ and 5.2, $p < 0.05$, df = 1; Fig. 1). Marten activity at resting sites was always of short duration (on average 0.3–1.1% of all fixes in 2-h periods, ie 5–24 min/day) with the exception of females in spring (on average 3.6% of fixes, ie 51 min/day; Fig. 1).

In all seasons daily ambient temperatures are lowest between 03.00–06.00 h. The daily activity pattern of both males and females was not positively related to the diurnal course of temperature (Kendall's coefficient of rank correlation: for males from –0.27 to –0.30; for females from 0.09 to 0.24; $p > 0.05$). However, between 04.00 and 08.00 h, when ambient temperature was at its lowest, martens often decreased their activity (especially females in spring).

For breeding females activity rhythms changed during the course of pregnancy and nursing. Indeed, in the last month of her pregnancy, female 6 was even active between 14.00–06.00 h (Fig. 2). During the first month of the cubs' life, activity rhythms of all lactating females showed two peaks and similarly all females decreased their activity between 02.00 to 10.00 h. In the same period, however, females were generally more active at their resting sites, especially between 06.00–22.00 h. Periods of activity at the resting site decreased during the second month of the cub's life and two females were again active outside the resting site between 14.00–02.00 h (Fig. 2).

On average, martens started their activity 73 min (SD ± 209) before sunset and terminated it 87 ± 245 min after sunrise. However, the onset and cessation of activity was highly variable according to both sex and season (Table 1). Overall females started their activity earlier than males (two-way Kruskal-Wallis ANOVA: $H = 6.4$, $p < 0.01$) and both sexes started activity earlier in summer and later in winter ($H = 45.9$, $p < 0.001$). Males and females both terminated activity at the same time ($H = 0.05$, ns) with termination time later in summer than in winter ($H = 40.1$, $p < 0.001$; Table 1).

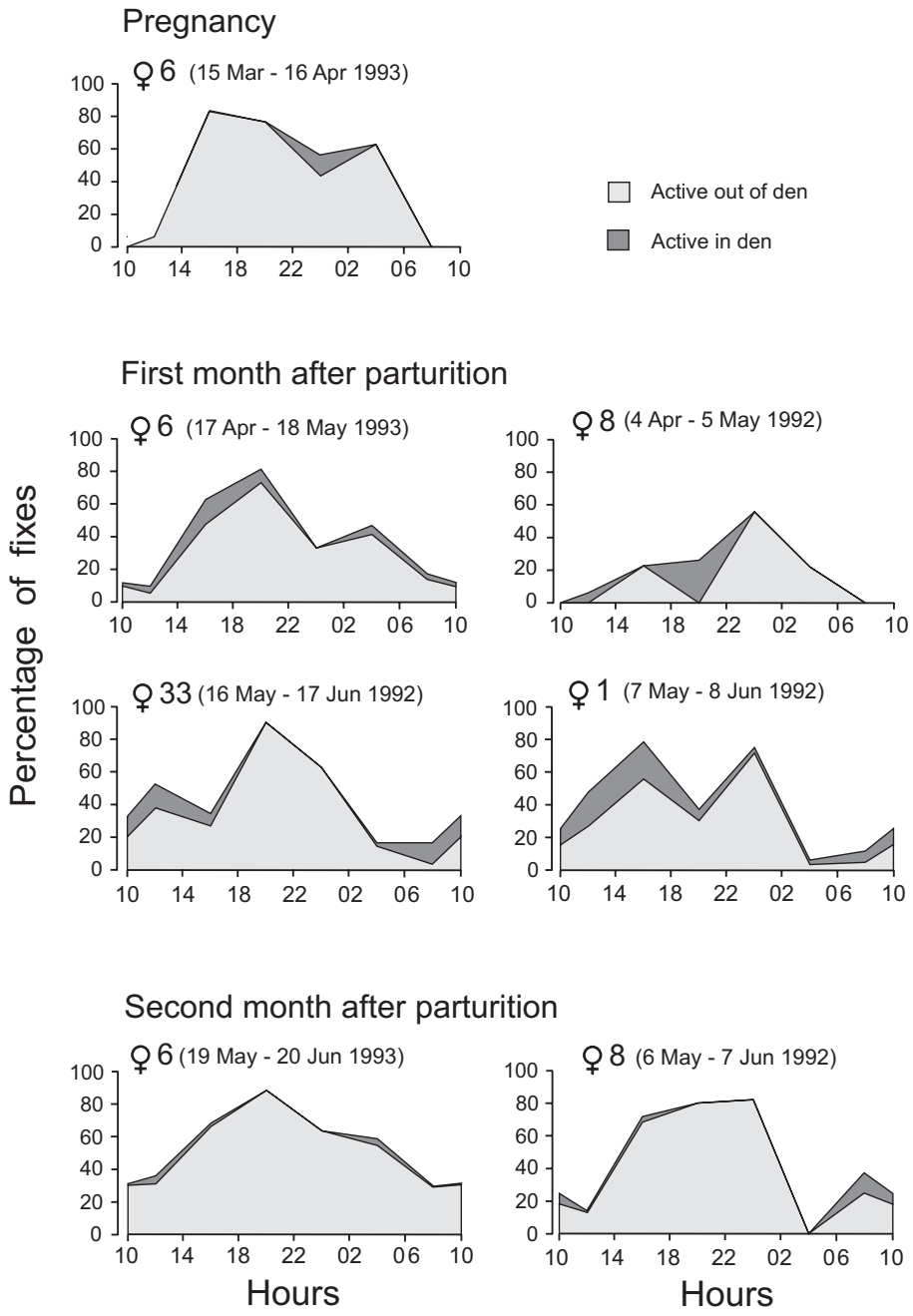

Fig. 2. Circadian activity rhythms of female pine martens during their pregnancy, the first and the second month after parturition in the Białowieża National Park. Total *n* fixes in 4-h periods varied from 40 to 150.

Table 1. Daily onset and cessation of activity period in relation to sunset and sunrise for pine martens *Martes martes* in the Białowieża National Park, 1991–1996. Positive and negative values indicate time (min) following and preceding sunset or sunrise, respectively. *n* – number of observation.

Sex of martens	Onset of activity in relation to sunset (minutes)			Cessation of activity in relation to sunrise (minutes)		
	n	Average	(SD)	*n*	Average	(SD)
			Spring			
Males	17	+90	(178)	17	+113	(185)
Females	21	+210	(151)	16	+113	(275)
			Summer			
Males	27	+125	(137)	23	+224	(143)
Females	7	+250	(166)	14	+254	(170)
			Autumn–winter			
Males	16	–190	(208)	19	–76	(128)
Females	12	–55	(94)	11	–209	(292)

Discussion

The results show that the activity rhythms of pine martens varied significantly between sexes and seasons. The differences between sexes could be due to differences in the reproduction investment of both sexes and this was most evident during spring. In this season, females care for their cubs (Grakov 1981). They leave the cubs for short bouts because unattended cubs may be susceptible to thermal stress (Frost and Krohn 1997). In spring, the activity of females was more evenly distributed throughout the day than that of males. Similar behaviour has been observed in females of other predator species (Paragi *et al*. 1994, Lariviere and Messier 1997). The even distribution of female activity during this season was apparently related to their care for young, thus producing more frequent activity bouts in a day, although each bout was of shorter duration than those of males (Zalewski 2000). However, both sexes were active for a similar duration (Zalewski 2000). Therefore, female activity started earlier in the day compared to males because they often had breaks in their activity to care for their cubs. In spring, females decreased their activity during the coldest part of the day (04.00–08.00 h) returning to their den at that time. This was particularly marked during the first month of a cub's life. In spring, females were also active longer in dens than at any other season, especially during the first month of cub's life. Females choose breeding sites in high cavities of trees (Zalewski 1997), where the risk of predation is low. These sites are accessible only to other martens. It is possible that reversal of activity between males and females is affected by male predation on cubs. However, there is no evidence of intraspecific predation. In America, male martens were

observed in breeding dens, scent marking or robbing the female of her prey, but not killing cubs (Jones *et al*. 1997). In summer, both males and females synchronized their activity pattern due to mating season.

In the Białowieża National Park, the daily activity pattern of both males and females were not related to the diurnal course of temperature during any season. In Ontario, American martens experiencing severe weather conditions remained in their resting sites all night and confined much of their activity to daylight hours when temperature were highest (Thompson and Colgan 1991). In California, the winter activity of martens was distributed more homogeneously throughout 24 h cycles (Zielinski *et al*. 1983, Martin 1987). In BNP, pine martens were only active during the night in the winter, despite the fact that temperatures were lowest then. In winter, however, females decreased their activity in colder periods of the night. Other studies have recorded only nocturnal activity amongst pine marten populations (Marchesi 1989). Drew and Bissonette (1997) suggest that the avoidance of daylight by American martens was due to higher predation risk. This explanation cannot be applied to pine martens in BNP. European pine martens are killed by the lynx *Lynx lynx*, red fox *Vulpes vulpes* or large raptors (Nyholm 1970, Korpimäki and Norrdahl 1989, Pulliainen 1981, Lindström *et al*. 1995, Okarma *et al*. 1997). In BNP, most of raptors are absent in winter (Pugacewicz 1996), while lynx and red fox are mainly nocturnal (Schmidt 1999, R. Kowalczyk, pers. comm). In winter, therefore, predation risks for martens seems to be even higher at night.

It is often assumed that predators synchronise their activity rhythms with that of their main prey (Ables 1969, Mikkola 1970, Curio 1976, Zielinski *et al*. 1983, Weber *et al*. 1994, Lodé 1995). Yellow-necked mice *Apodemus flavicollis* were active at night (Buchalczyk 1964, Wójcik and Wołk 1985) and the activity pattern of pine martens correlated with that of this species. However, martens consistently preyed on mice less than could have been expected from the proportion of mice in the total biomass of forest rodents determined by trapping (Jędrzejewski *et al*. 1993). This suggests that the activity rhythms of both predator and prey are not related but depend on other factors and synchronisation of predator-prey patterns of activities do not implicate predator specialisation in this prey. Bank vole are the preferred prey species by pine marten (Jędrzejewski *et al*. 1993). In spring and summer, bank voles showed activity patterns with several peaks throughout the day and night (Buchalczyk 1964, Wójcik and Wołk 1985). During these two seasons, the activity patterns of both male and female pine martens did not synchronise with those of bank voles. In autumn, however, bank voles' activity displayed two peaks: at 18.00–20.00 h and 04.00–08.00 h (Buchalczyk 1964, Wójcik and Wołk 1985). This coincided with the circadian rhythm of pine marten activities (especially males) at this time of year.

In conclusion, reproduction clearly affected the intersexual variation in the circadian rhythm of marten activity. However, marten activity behaviour does not clearly relate to the activity rhythms of its main prey nor to thermal stress. There is no evidence either to suggest that martens are active at night to avoid predation.

Acknowledgements: I wish to thank the technical staff of MRI (E. Bujko and K. Zub), students of Farnborough College of Technology (England), Warsaw University, the Jagiellonian University in Kraków, and Earthwatch Research Corps for their help in field work. Special thanks go to Dr B. Jędrzejewska for her help in the preparation of this manuscript. My thanks to Prof S. W. Buskirk and Z. Pucek for their comments on an earlier draft. The study was supported partly by the Mammal Research Institute PAS budget and partly by a KBN 6 P205 080 06 grant.

References

Ables E. D. 1969. Activity studies of red foxes in Southern Wisconsin. The Journal of Wildlife Management 33: 145–153.

Aschoff J. 1964. Survival value of diurnal rhythms. Symposia of the Zoological Society of London 13: 79–89.

Aschoff J. 1966. Circadian activity pattern with two peaks. Ecology 47: 657–662.

Buchalczyk T. 1964. Daily activity rhythm in rodents under natural conditions. Acta Theriologica 9: 357–362.

Curio E. 1976. The ethology of predation. Springer-Verlag, Berlin, Heidelberg, New York: 1–250.

Daan S. and Aschoff J. 1982. Circadian contributions to survival. [In: Vertebrate circadian systems. J. Aschoff, S. Daan and G. A. Groos, eds]. Springer-Verlag, Berlin, Heidelberg, New York: 305–321.

Drew G. S. and Bissonette J. A. 1997 Winter activity patterns of American martens (*Martes americana*): Rejection of the hypothesis of thermal-cost minimization. Canadian Journal of Zoology 75: 812–816.

Faliński J. B. 1986. Vegetation dynamics in temperate lowland primeval forest. Dr. W. Junk Publishers, Dordrecht: 1–537.

Ferguson J. W. H., Gaplin J. S. and De Wet M. J. 1988. Factors affecting the activity patterns of black-backed jackals *Canis mesomelas*. Journal of Zoology, London 214: 55–69.

Frost H. C. and Krohn W. B. 1997. Factor affecting the reproductive success of captive female fisher. [In: Martes: taxonomy, ecology, techniques, and management. G. Proulx, H. N. Bryant and P. M. Woodard, eds]. Provincial Museum of Alberta, Alberta, Canada: 329–349.

Geffen E. and Macdonald D. W. 1993. Activity and movement patterns of Blanford's foxes. Journal of Mammalogy 74: 455–463.

Gerell R. 1969. Activity patterns of the mink *Mustela vison* Schreber in southern Sweden. Oikos 20: 451–460.

Grakov N. N. 1981. Lesnaya kunitsa [The pine marten]. Nauka, Moskva: 1–109. [In Russian]

Iversen J. A. 1972. Basal energy metabolism of mustelids. Journal Comparative Physiology 81: 341–344.

Jędrzejewska B. and Jędrzejewski W. 1998. Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. Springer-Verlag, Berlin, Heildelberg, New York: 1–450.

Jędrzejewski W., Zalewski A. and Jędrzejewska B. 1993. Foraging by pine marten *Martes martes* in relation to food resources in Białowieża National Park, Poland. Acta Theriologica 38: 405–426.

Jones L. L. C., Raphael M. G., Forbes J. T. and Clark L. A. 1997. Using remotely activated cameras to monitor maternal dens of martens. [In: Martes: taxonomy, ecology, techniques, and management. G. Proulx, H. N. Bryant and P. M. Woodard, eds]. Provincial Museum of Alberta, Alberta, Canada: 329–349.

Koop K. and Velimirov B. 1982. Field observations on activity and feeding of bat-eared foxes (*Otocyon megalotis*) at Nxai Pan, Botswana. African Journal of Ecology 20: 23–27.

Körpimaki E. and Norrdahl K. 1989. Avian predation on mustelids in Europe 1: occurrence and effects on body size variation and life traits. Oikos 55: 205–215.

Lariviere S. and Messier F. 1997. Seasonal and daily activity patterns of striped skunks (*Mephitis mephitis*) in the Canadian prairies. Journal of Zoology, London 243: 255–262.

Lindström E. R., Brainerd S. M., Helldin J. O. and Overskaug K. 1995. Pine marten – red fox interactions: A case of intraguild predation? Annales Zoologici Fennici 32: 123–130.

Lodé T. 1995. Activity pattern of polecats *Mustela putorius* L in relation to food habits and prey activity. Ethology 100: 295–308.

Marchesi P. 1989. Ecologie et comportement de la martre (*Martes martes* L.) dans le Jura Suisse. Ph D thesis, University of Neuchâtel, Neuchâtel: 1–185.

Martin S. K. 1987. The ecology of the pine marten (*Martes americana*) at Sagehen Creek, California. Ph D thesis, University of California, Berkeley: 1–223.

Mikkola H. 1970. On the activity and food of the pygmy owl *Glaucidium passerinum* during breeding. Ornis Fennica 47: 10–14.

Nyholm E. S. 1970. On the ecology of the pine marten (*Martes martes*) in Eastern and Northern Finland. Suomen Riista 22: 105–117.

Okarma H., Jędrzejewski W., Schmidt K., Kowalczyk R. and Jędrzejewska B. 1997. Predation of Eurasian lynx on roe deer and red deer in Białowieża Primeval Forest, Poland. Acta Theriologica 42: 203–224.

Olszewski J. L. 1986. The role of forest ecosystems in modifying local climate of the Białowieża Primeval Forest, as revealed by air temperature characteristics. Polish Academy of Sciences, Ossolineum, Wrocław: 1–222.

Paragi T. F., Arthur S. M. and Krohn W. B. 1994. Seasonal and circadian activity patterns of female fishers, *Martes pennanti*, with kits. Canadian Field Naturalist 108: 52–57.

Pugacewicz E. 1996. Birds of prey breeding in the Polish part of the Białowieża Primeval Forest. Notatki Ornitologiczne 37: 173–224. [In Polish with English summary]

Pulliainen E. 1981. Winter habitat selection, home-range, and movements of the Pine marten (*Martes martes*) in Finnish Lapland Forest. [In: Worldwide Furbearer Conference Proceedings. J. A. Chapman and D. Pursley, eds]. Frostburg, Maryland USA: 1068–1087.

Schmidt K. 1999. Variation in daily activity of the free-living Eurasian lynx (*Lynx lynx*) in Białowieża Primeval Forest, Poland. Journal of Zoology, London 249: 417–425.

Schuh J., Tietze F. and Schmidt P. 1971. Beobachtungen zum Aktivitätsverhalten der Wildkatze (*Felis silvestris* Schreber). Hercynia 8: 102–107.

Thompson I. D. and Colgan P. W. 1991. Optimal foraging by *Martes americana*: the role of large prey in winter. [In: Global trends in wildlife management. B. Bobek, K. Perzanowski and W. Regelin, eds]. Świat Press, Kraków, Warszawa: 173–176.

Weber J. M., Meia J. S. and Aubry S. 1994. Activity of foxes, *Vulpes vulpes*, in the Swiss Jura Mountains. Zeitschrift für Säugetierkunde 59: 9–13.

Wójcik J. M. and Wołk K. 1985. The daily activity rhythm of two competitive rodents: *Clethrionomys glareolus* and *Apodemus flavicollis*. Acta Theriologica 30: 241–258.

Zalewski A. 1997. Factors affecting selection of resting site type by pine marten in primeval deciduous forests (Białowieża National Park, Poland). Acta Theriologica 42: 271–288.

Zalewski A. 2000. Factor affecting the duration of activity by pine martens (*Martes martes*) in Białowieża National Park, Poland. Journal of Zoology, London 251: 439–447.

Zielinski W. J., Spencer W. D. and Barrett R. H. 1983. Relationship between food habits and activity patterns of pine martens. Journal of Mammalogy 64: 387–396.

Received 1 June 2001, accepted 22 June 2001.