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Late winter social activity in pine marten (*Martes martes*) — false heat or dispersal?

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In late winter (February–March) the social behaviour of the pine marten (*Martes martes*) is intensified (increased scent marking frequency, intersexual tolerance and intrasexual aggression) and the levels of sex hormones are increased, i. e. the same characteristics as for the mating period in July–August (pine marten exhibits delayed implantation). However, in late winter no fertilizations are possible, since males have no spermatogenesis at this time. Here, we review data on this "false heat", including some of our own observations. We suggest that late winter is the start of a dispersal period for pine marten, and that the main function of the social activity is territorial defence. The period coincides with the implantation and the beginning of the active pregnancy. This change in the female's reproductive cycle may start the behaviour of driving out her young from the territory, and by that, the whole dispersal mechanism.

1. Introduction

The intensified social behaviour and activity of pine marten (*Martes martes*) in late winter (February–March) have for long been known among hunters and fur farmers (Prell 1927, Schmidt 1934). This temporary sociality occurs 1–2 months before parturition, and was until the 1930's interpreted as mating behaviour (reviewed by Schmidt 1943). Later, it has been made clear that pine martens mate only in late summer (the implantation is delayed 7 months; Canivenc & Bonnin 1975); summer is the only time of the year when true matings are observed (Prell 1927, Schmidt 1934) and when spermatogenesis occurs (Schmidt 1943, Danilov & Tumanov 1972, Audy 1976). Still, the social activities in late winter are sometimes mentioned in literature, but no one has presented a satisfactory explanation of their adaptive value.

In this paper, we compile scattered data on behaviour and physiology of pine marten in late winter, including some of our own unpublished observations. We review and evaluate the explanations of the late winter social behaviour proposed in literature, and develop a hypothesis on marten dispersal.

2. Behaviour and physiology in late winter

For pine martens, February–March is the time of implantation, and the beginning of active preg-

nancy (Canivenc & Bonnin 1975, Mead 1994). In connection with implantation, *corpora lutea* increase in size (Canivenc & Bonnin 1975), the progesterone level rises (Canivenc & Bonnin 1975), and possibly also the estrogen level (it does for sables, *M. zibellina*; Polyntsev et al. 1975, Shul'gina et al. 1981). Whether the external genitals of the female are affected by the increase in sex hormones is not clear. Schmidt (1934) state that the vulvae of both pine martens and sables remain small and dry throughout this period, whereas Kler (1941, in Pawlinin 1966) found a vulval enlargement in sables.

In males, testes start to grow slowly, but there is a dramatic increase in the size of the testosterone producing Leydig cells, and the testosterone level seems to peak (Audy 1976).

During late winter, caged pine martens have an excited and "restless" behaviour, with chasing and playing (Prell 1927, Schmidt 1934, 1943) and with fighting between animals of the same sex (Schmidt 1943). They show an increased interest in the opposite sex, and may do short mating attempts (however futile; Prell 1927). There are also some observations of free-ranging animals following each other at this time (Schmidt 1934, 1943, Krott 1973, de Jounge 1979, Marchesi 1989), and one record of a male and a female sharing food (Krott 1973). The intensity of scent marking increases considerably in both sexes, particularily abdominal gland rubbing, but also urination (Pulliainen 1982, Grünwald 1988).

This increased social activity resembles that of the mating period in June–August (Schmidt 1934), and is often labeled "false heat" (e.g., Schmidt 1943, Audy 1976). Also during the true heat in summer, pine martens have increased levels of sex hormones (Audy 1976), and they show intensified activity and social behaviour (Prell 1927, Schmidt 1934, 1943, Krott 1973), including scent marking (Grünwald 1988).

3. Review of hypotheses

Some kind of social activity in late winter is also reported for sable (Pawlinin 1966), American marten (*M. americana*; Ashbrook & Hanson 1930, Markley & Bassett 1942), and stone marten (*M. foina*; Schmidt 1943). These, and the Japanese marten (*M. melampus*), are closely related to the pine marten (Anderson 1994), and show many similarities in ecology and behaviour. Thus, we reviewed literature on them all (except Japanese marten, for which no relevant literature could be found), in search for hypotheses to explain this phenomenon. Three main ideas were found.

3.1. False heat in a strict sense

Schmidt (1943) explained the social activity of pine (and stone) martens in late winter simply as a secondary effect of the regular yearly reproductive cycle. This was also suggested for sables by Monakhov and Timofejev (1963, in Pawlinin 1966). Females, influenced by the increased levels of hormones related to implantation, behave as if they were in heat. Males may be affected in a similar way, at the start of the development of the testes (Monakhov & Timofejev 1963, in Pawlinin 1966), or they may be affected by the false heat of the females (Schmidt 1943). But considering the large costs that presumably are associated with the activities (chasing, fighting and scent marking), we find the behaviour less likely to be of no function and, thus, non-adaptive.

3.2. Establishment of a pair bond

Krott (1973), Madsen & Rasmussen (1985) and Selås (1991) meant that the contacts between the sexes of pine (and stone) marten in late winter are a (re-)establishment of a pair bond, either for cooperative feeding (Krott 1973), or for cooperative rearing of the young (Krott 1973, Madsen and Rasmussen 1985). However, the only observations that support this are indicative (Krott 1973), and for pine marten, a lack of such cooperative behaviour is reported (Schmidt 1943, Pulliainen 1981, Marchesi 1989).

3.3. Territoriality and dispersal

Gusev (1961) and Jensen & Jensen (1970) stressed the importance of territoriality and dispersal to explain the late winter social behaviour in martens, although they did it on somewhat

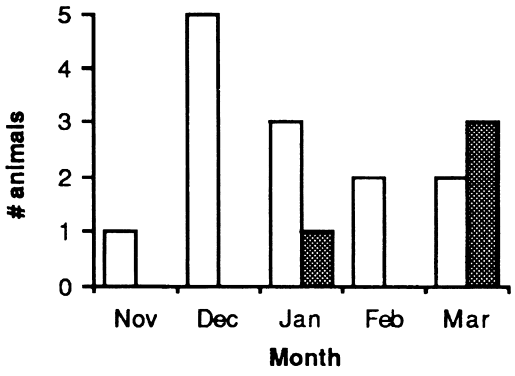

Fig. 1. Captures of pine martens (n = 17) by month, at Grimsö Wildlife Research Station, Sweden, and spacial status of the radio-collared animals during the months immediately after capture. Residents (white bars) used an area of <20 km^2 in a regular manner, around or adjacent to the place of capture. Transients (grey bars) travelled several kilometers away from the place of capture, dispersing by intervals, and with a total activity area exceeding 40 km^2. All transients were juveniles (<1 yr age).Three included (resident) martens are from Storch (1988). Traps were only set from November-March. Details of study area and methods are given by Brainerd et al. (1994).

different basis. Gusev interpreted the late winter social behaviour and activity in sables as starvation-related dispersal. This does not explain the behaviour also among caged animals, not living under nutritional stress. Jensen & Jensen suggested that stone martens establish territories before parturition, which would cause the late winter activity (and aggression). However, they did not present any data to support this hypothesis, and martens are generally considered to have stable territories year-round (Powell 1979).

4. Development of the dispersal hypothesis

Although the ideas of Gusev and Jensen & Jensen may not apply in detail, there are observations supporting the general notion that territoriality and dispersal are important features of pine marten behaviour in late winter. Usinger (1935, in Schmidt 1943) noted an occurrence of young pine martens in late winter, in areas where no martens were observed before January, and interpreted it as immigration. In our radio-tracking study at Grimsö Wildlife Research Station in south-central Sweden, transient pine martens were caught only in January–March (Fig. 1).

For stone martens, Skirnisson (1986) suggested that the time for dispersal of young varies, occuring either in fall or after the winter. Archibald & Jessup (1984) reported two periods of dispersal in American martens: the first period in late summer and fall, coinciding with estrus, and including mainly juveniles; the second period probably in early spring, and including animals of different ages. This may apply also to pine marten. Such dual dispersal implies tolerance of adults towards juveniles in winter, which was reported by Pulliainen (1981) and Kvalheim (1982), and also found in our study (unpubl.).

It has been assumed, that young pine martens disperse in late summer and fall, when they become independent of their mother (e.g., Schmidt 1943, Krott 1973). We argue, that they may stay overwinter in their natal territory, as subordinates, and start their dispersal in late winter. There are certain advantages of such a post-winter dispersal:

a) Spending the first winter in a familiar area will probably increase hunting success in general.
b) Pine martens cache food (particularily eggs) during summer and eat it in winter (e. g. Storch et al. 1990). Even if juveniles are too young to cache food during most of the summer, adults may perhaps share the cached food with their offspring. To be able to utilize these cashes, animals have to stay overwinter in the same area as they spent the summer.
c) Assuming that the cost of having subordinates is relatively low, adults may also benefit from better survival of their young.
d) Pine martens have late sexual maturity (≥15 months age; Danilov & Tumanov 1972, 1975), and even after their first winter, young martens have >4 months to find and establish a territory, before their first mating season.

Dispersal and increased territoriality in late winter would explain much of the "false heat" phenomenon, such as increased activity, aggression towards the same sex (pine martens are intrasexually territorial; e.g., Marchesi 1989), and scent marking, all governed by the increased lev-

els of sex hormones. However, other mechanisms may be partially responsible for the observed behaviours; e.g., increased luteal hormone levels, primarily aimed at controlling implantation and active pregnancy, may start the female's behaviour of driving out her young, and by that, induce the whole dispersal mechanism. Increased hormone levels may also result in the observed attraction between the sexes, which otherwise remains unexplained by our hypothesis.

Also among the other four closely related martens, i. e. sable, American marten, Japanese marten and stone marten, dispersal may explain increased social activity in late winter. In the reviewed literature, nothing has been found that contradicts this notion.

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