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SHORT COMMUNICATION

“False heat,” big testes, and the onset of natal dispersal in European pine Martens (*Martes martes*)

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Abstract Natal dispersal plays a central role in population biology, ecology, and evolution. Therefore, describing dispersal patterns including dispersal rate, onset, duration, and distance and investigating its main ecological and phenotype correlates are of prime importance. Dispersal data are scarce in rare and elusive carnivores such as mustelids and notably in European pine Marten *Martes martes*. Natal dispersal is mostly thought to occur in late winter either as a consequence of offspring eviction by adult females experiencing a “false heat” period related to the delayed implantation of embryos or as a consequence of physiological changes in offspring related to sexual maturation. Nineteen juvenile and subadult pine martens were monitored by telemetry during their first year of life to describe the dispersal pattern, in particular, to investigate the onset of natal dispersal. Only 13 out of the 19 pine martens monitored gave reliable information, and seven out of them (53.85 %) dispersed. No sex bias either in dispersal rate, distance, or duration was evidenced. As expected, all dispersers whatever their sex left their natal area in a relatively narrow period of 1 month in late winter (February 17th–March 17th). This period did not match with any body mass variation but was clearly synchronous with an increase in testis mass. Our results confirmed that this late winter period is very intense in terms of social interactions and physiological changes in the European pine marten. Last, they also pointed out that human-induced mortality of dispersers in late winter could be high so that late winter might be a focus period for management actions.

Keywords *Martes martes* · European pine marten · Natal dispersal · Dispersal onset · Telemetry

Introduction

Natal dispersal, defined as the movement made by an individual from its birthplace to the place of first reproduction (Howard 1960), is a widespread behavioral process. Its crucial role in population biology, ecology, and evolution is now widely recognized albeit natal dispersal remains poorly understood. Considerable knowledge has been gained since evolutionary ecologists have started to sequence natal dispersal behavior in three successive behavioral stages (Travis et al. 2012): emigration (also called onset, timing of dispersal), transience (also called transfer), and immigration (also called settlement). There is now considerable evidence that the decision to leave or to stay, to make a short or large movement, and to settle or not in a given place are not influenced by the same ultimate and proximate factors. Both internal, sensu phenotype-dependent, and environmental, sensu condition-dependent, factors trigger dispersal and interact in complex ways (Clobert et al. 2001). It is thus becoming of prime importance to investigate each stage apart from the others to better understand the dispersal processes in wild populations as much as its consequences on individual fitness (Bonte et al. 2012) and on population dynamics and genetics. The basic dispersal pattern of mammalian solitary carnivores, i.e., sex

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and age variations in dispersal rate and distance, has received as much attention as in other taxonomic groups, but the detailed process of natal dispersal within the three behavioral stages framework mentioned above is poorly known, especially in mustelids (Arthur et al. 1993). The European pine marten (*Martes martes*) is one of the species for which almost nothing is known about natal dispersal. Although it is usually thought that most of the young individuals disperse either in early fall or in early spring (Helldin and Lindström 1995 and references therein), few studies, to our knowledge, have reported natal dispersal movements (e.g., Helldin and Lindström 1995; Zalewski 2012) and have given any basic characteristics of the dispersal pattern. Helldin and Lindström (1995) suggested likely associations between condition-dependent or phenotype-dependent factors and the onset of natal dispersal in pine martens. Indeed they reviewed evidences that a "false heat," i.e., an increase in social activity and agonistic intrasexual interactions, occurred in February and March. One hypothesis to explain this phenomenon might be related to the yearly reproductive cycle of adult females. Indeed, this February–March period corresponds to the restart of gestation, following a delayed implantation of blastocysts. As a result, adult females could evict their young, forcing them to disperse during this period. They also discussed the possibility that this false heat resulted mostly from the beginning of the dispersal period simultaneous to a physiological change of young individuals, namely an increase of sex hormone concentrations. In both hypotheses, young martens should predominantly disperse in February–March. Studies in mammals have shown that the onset of natal dispersal is often correlated with both morphological and physiological changes (e.g., threshold body mass hypothesis, in roe deer *Capreolus capreolus*, Wahlström 1994; "ontogenic switch hypothesis," in Belding's ground squirrels *Spermophilus beldingi*, Nunes and Holekamp 1996; but see Elliot et al. 2014), making individuals either likely competitors for adults or able to bear dispersal costs. Here, we investigated the onset of natal dispersal in first-year pine martens using telemetry monitoring and specifically assessed whether the natal dispersal onset occurred in late winter (mid-February to March) as suggested by Helldin and Lindström (1995). Using data from dead recoveries of first-year pine martens of both sexes, we also evaluated the association between the onset of dispersal and the phenologies of body mass and testes mass over the first year of life.

Material and methods

From a larger telemetry dataset (n=44 individuals of all ages), we selected only those that were captured as juveniles or subadults between July and February 15th of the year after their birth year (i.e., between 4 and 11.5 months old assuming a common birth date of April 1st). Hence, two juvenile ([4–6] months old, both males) and 17 subadult ([6–11.5] months old, eight males, nine females) pine martens were retained to investigate the timing of dispersal. Individuals were trapped in box cages in the region of Bresse (study area=911 km^2, eastern France 5° 13′ E, 46° 27′ N) over four winters (electronic supplementary material Table S1), where hunting and trapping is legally allowed. Animals were anesthetized by intramuscular injection of Domitor® (10 mg kg^{-1}, medetomidine, Pfizer Animal Health, New York, USA) and revived with Antisédan® (atipamezol, Pfizer Animal Health, New York, USA) to ensure a quick reversal of sedation. We marked each individual with a transponder (Allflex®, Vitré, France) and radio-collared them before release at their site of capture. Collars were TXH-2 from Televilt® (Stockholm, Sweden) or TW-5 with a biothane collar from Biotrack Ltd® (Wareham, Dorset, UK) and weighed about 32 g. Age was estimated from a set of morphological variables (body mass, tooth wear, body length, tail length, neck circumference, posterior foot length, and baculum length for males, Ruette et al. unpublished data) and confirmed by the number of annual growth lines visible in the tooth cementum using a standardized cementum aging model for each species (Matson's Laboratory, Milltown, MT, USA, Matson and Matson 1993) when martens were later recovered dead (11 out of the 19, electronic supplementary material Table S1).

The pine martens were located at least twice a week when they were resting during the day, with a precision higher than 100 m. For this sample (n=19), the mean duration of monitoring was 122±99 days (8–379 days, electronic supplementary material Table S1) and the mean number of locations was 39.6±30.56 (6–120 locations). Based on their successive locations, we assessed whether each individual dispersed or not, assuming that the capture location was close to the birth site. Each individual was classified into philopatric ("stationary" or "explorer") or disperser ("shifter" or "one-way") following the initial classification of McShea and Madison (1992), adapted to pine martens (electronic supplementary material).

We applied the k-means clustering method (Forgy 1965) on individual locations of the dispersers only (both shifter and one-way individuals) to identify two successive spatial clusters over the monitoring, namely, the areas used for resting before and after the natal dispersal (electronic supplementary material Fig. S1). We then defined the departure date, i.e., the timing of dispersal, as the date of the last location in the first locations' cluster and the settlement date as the date of the first location in the second cluster. We finally estimated the natal dispersal distance by computing the Euclidean distance between the centroids of the two spatial clusters. Dispersal duration, i.e., the length of the transience phase, was computed as the difference (in days) between the settlement date and the departure date.

During the study period, 59 male and 32 female pine martens aged less than 18 months were collected dead on the study area from trappers and hunters. Age in days was then estimated by the difference between the recovery date and April 1st. The dead animals were weighed and aged as above. For males, the testes were extracted from the corpse and weighed (n=36 out of the 59). This allowed us to assess the age variation of both testes mass and body mass in both sexes during the first year of life.

Results

Captures mostly occurred from early December to late January (16 out of 19, electronic supplementary material Table S1) which precluded a reliable assessment of dispersal in early fall. The two juveniles monitored during this early fall period did not disperse, one was still philopatric at the end of its monitoring, and the second dispersed during the mid-February to March period (see below, electronic supplementary material Table S1). As regards dispersal during the second focused period of mid-February to March, six individuals (three males, three females) could not be classified: either because their monitoring duration was less than 30 days (four out of the six) or because their monitoring ceased long before this period (one out of the six) or because it ceased during an exploration movement (Fig. 1a, one out of the six, electronic supplementary material Table S1). Among the 13 remaining individuals, five were classified as philopatric explorer (two males, three females), i.e., they made exploration movements but always returned soon after to their birthplace (Fig. 1b), and one was classified as a philopatric stationary individual. However, the monitoring of four out of these six individuals ceased between March 1st and March 17th (electronic supplementary material Table S1), right in the middle of the focused period so that we could not rule out that they would have dispersed later (Fig. 1c).

The seven remaining individuals were classified as dispersers (Fig. 2a), either shifter individuals (one male, one female) or one-way individuals (three males, two females). The overall natal dispersal rate was 7/13=53.85 %. For these seven dispersers, the natal dispersal distance ranged from 2256 to 17,257 m and was not significantly different in both sexes (4968±2057 m in females, 7028±7058 m in males).

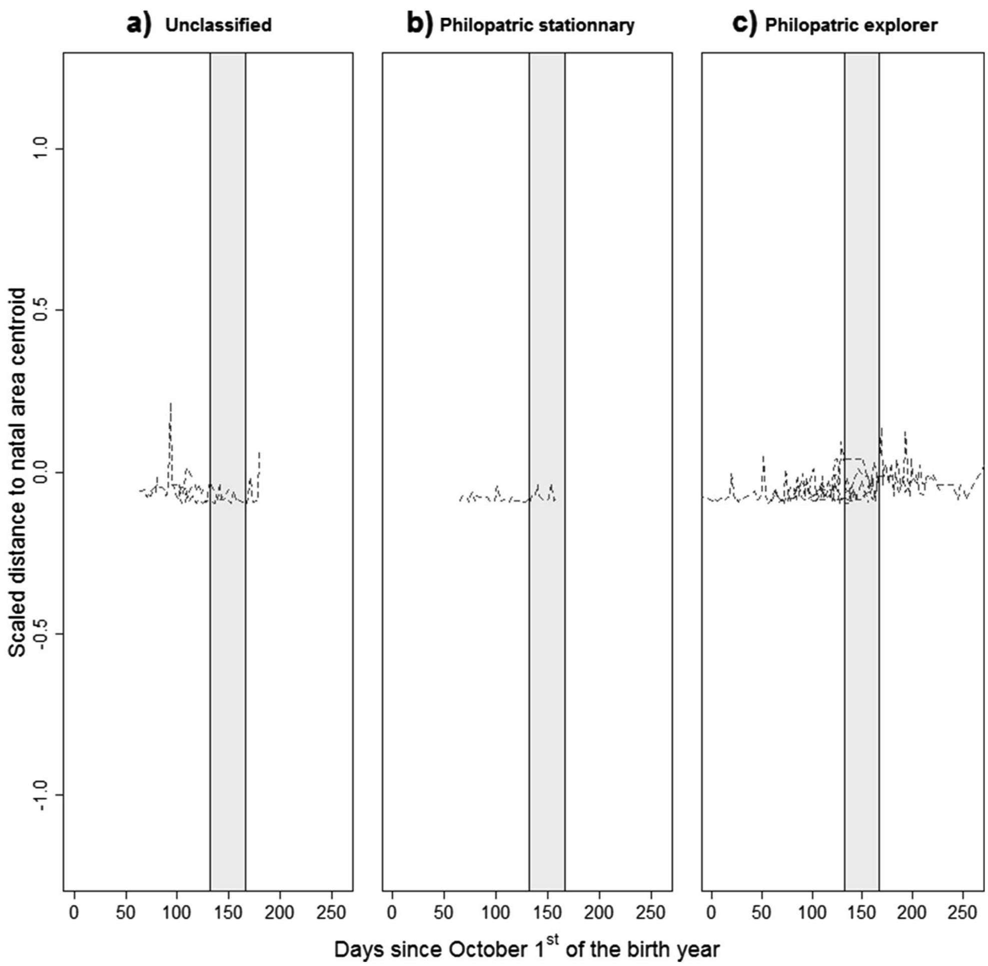

Fig. 1 Temporal evolution of the scaled distance between each successive location and the centroid of the natal area from October 1st of the the year of birth to the end of June the following year, **a** unclassified pine martens; **b** stationary pine martens; **c** explorer pine martens

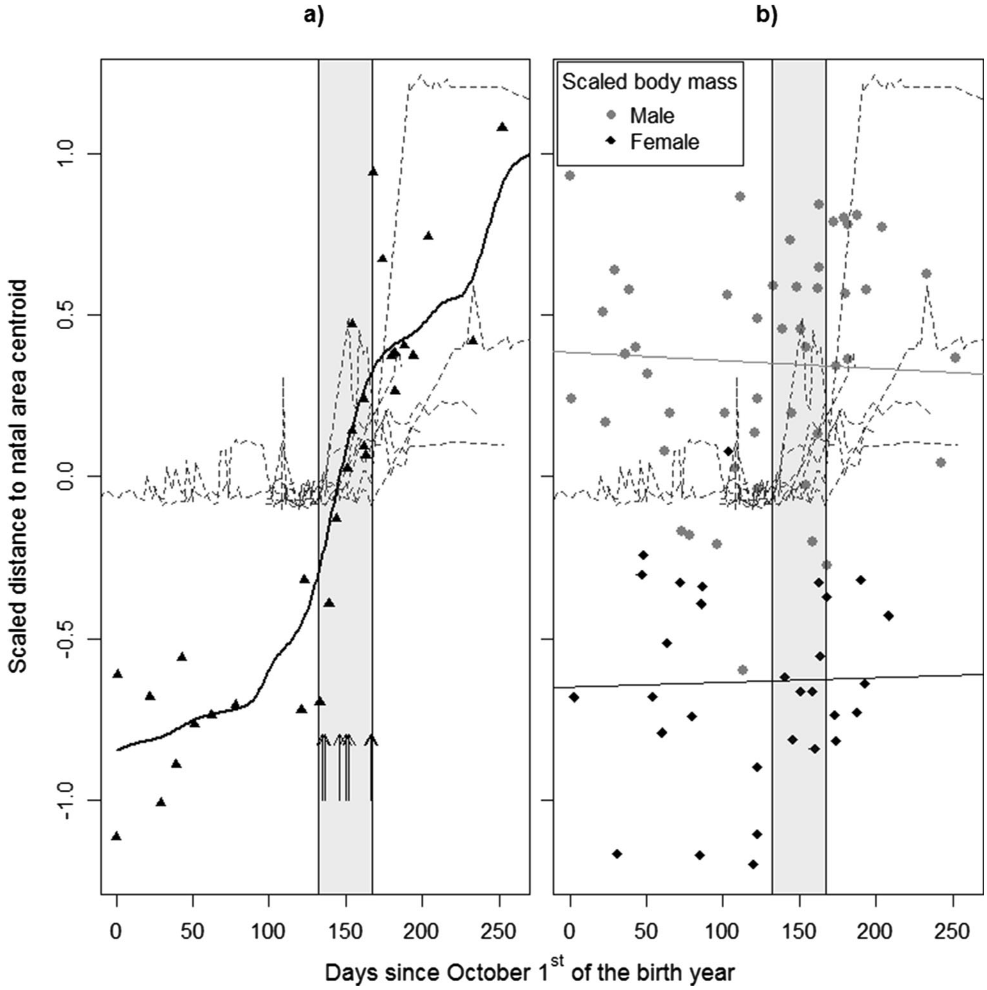

Fig. 2 **a** Coincidence between the temporal evolution of the scaled distance between each successive location and the centroid of the natal area for dispersing pine martens and the phenology of the averaged testis mass (n=36) from October 1st of the year of birth to the end of June the following year. Testis mass was standardized for body mass using the residuals of the linear model between the log-testis mass and the log-body mass. Testis mass was scaled to facilitate graphical display. **b** Temporal variation of male (n=58) and female (n=32) body mass from October 1st of the year of birth to the end of June the following year

The natal dispersal duration ranged from 5 to 76 days and did not differ between sexes (35±36 days in females, 29±17 days in males). All the dispersers started their natal dispersal movement 15 days around March 1st the year after their birth (Fig. 2a, electronic supplementary material Table S1). This relatively narrow period for the timing of dispersal was clearly associated with the onset of relative testes mass increase in subadult males (Fig. 2a) and did not match with any age variation of body mass in both subadult males and females (Fig. 2b).

Discussion

Emigration movements, sensu departure from the natal area, were highly synchronous and occurred within a narrow period of less than one month between February 17th and March 17th. Although we cannot rule out that we could have missed dispersal movements in early fall (only two individuals were monitored during this period, most individuals were captured after December 1st), this finding is in agreement with the idea that natal dispersal mostly occurs in late winter (Helldin and Lindström 1995). Both males and females dispersed during this period without any variation in body mass as subadult pine martens reach adult size when they are 6 to 8 months old (Ruette et al. unpublished data). Such synchronous dispersal is in agreement with the first hypothesis of Helldin and Lindström (1995) which argued that hormonal changes accompanying the restart of gestation induce the adult female's behavior of driving out its young (sensu condition-dependent dispersal), independently of offsprings' phenotypes. Alternatively, the onset of dispersal of males matched very well with the increase of testis mass described on our transversal sample in late winter. Concomitantly with this increase, the level of testosterone is expected to reach its peak (Audy 1976). This result is in agreement with phenotype-dependent dispersal and would support the second hypothesis of Helldin and Lindström (1995), i.e., the false heat results from the whole dispersal process. We acknowledge that only longitudinal data on individuals would help to clarify this process. Unfortunately, we did not have any hormonal and morpho-anatomical metrics of such a physiological change in subadult females during this period. To our knowledge, we provided here the first evaluation of the two hypotheses of Helldin and Lindström (1995) about the false heat in *Martes* species in a wild population of pine martens since the paper of Helldin and Lindström (1995) has been published. Based on our study, it is not possible to rule out any of them, but data reported here provide the opportunity for the mustelids community to increase our common knowledge about this particular false heat pattern. Finally, highly synchronous natal dispersal in pine martens might have management implications. Natal dispersal plays a major role in ensuring connectivity between populations and/or recolonization of depleted sites (Clobert et al. 2001). In our area, human-induced mortality is mostly attributed to trapping/hunting and roadkills (Ruette et al. 2015). As trapping is mostly active between January and March in France, most of the animals caught might be crossing pine martens, especially since subadult martens are likely easier to trap than adults. Hence, late winter would be not only a critical period for pine marten populations but also the focus period to control human-induced mortality when necessary.

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References

Arthur SM, Paragi TF, Krohn WB (1993) Dispersal of juvenile fishers in Maine. J Wildl Manag 57:868–874

Audy MC (1976) Le cycle sexuel saisonnier du male des mustélidés Européens. Gen Comp Endocrinol 30:117–127

Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M, Gibbs M, Lehouck V, Matthysen E, Mustin K, Saastamoinen M, Schtickzelle N, Stevens VM, Vandewoestijne S, Baguette M, Barton K, Benton TG, Chaput-Bardy A, Clobert J, Dytham C, Hovestadt T, Meier CM, Palmer S, Turlure C, Travis J (2012) Costs of dispersal. Biol Rev 87:290–312

Clobert J, Danchin E, Dhondt AA, Nichols JD (2001) Dispersal. Oxford University Press, New York

Elliot NB, Valeix M, Macdonald DW, Loveridge AJ (2014) Social relationships affect dispersal timing revealing a delayed infanticide in African lions. Oikos 9:1049–1056

Forgy EW (1965) Cluster analysis of multivariate data: efficiency *vs* interpretability of classifications. Biometrics 21:768–769

Helldin JO, Lindström ER (1995) Late winter social activity in pine marten (*Martes martes*)—false heat or dispersal. Ann Zool Fenn 32:145–149

Howard W (1960) Innate and environmental dispersal of individual vertebrates. Am Midl Nat 63:152–161

Matson GM, Matson J (1993) Progress in cementum aging of martens and fishers. Special Report no. 931. Matson's Laboratory, p 3

McShea WJ, Madison DM (1992) Alternative approaches to study of small mammal dispersal: insights from radiotelemetry. In: Stenseth NC, Lidicker WZJ (eds) Animal dispersal: small mammals as a model. Chapman and Hall, p 365

Nunes S, Holekamp K (1996) Mass and fat influence the timing of natal dispersal in Belding's ground squirrels. J Mammal 77:807–817

Ruette S, Vandel J-M, Albaret M, Devillard S (2015) Comparative survival pattern of the syntopic pine and stone martens in a rural trapped area in France. J Zool

Travis JMJ, Mustin K, Bartoń KA, Benton TG, Clobert J, Delgado MM, Dytham C, Hovestadt T, Palmer SCF, Van Dyck H, Bonte D (2012) Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. Methods Ecol Evol 3:628–641

Wahlström LK (1994) The significance of male male-aggression for yearling dispersal in roe deer (*Capreolus capreolus*). Behav Ecol Sociobiol 35:409–412

Zalewski A (2012) Alternative strategies in the acquisition of home ranges by male pine martens in a high-density population. Acta Theriol 57:371–375