Large male territories in a low-density population of roe deer Capreolus capreolus with small female home ranges

Author: Mysterud, Atle

Source: Wildlife Biology, 4(4) : 231-235

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.1998.026

Large male territories in a low-density population of roe deer *Capreolus capreolus* with small female home ranges

Atle Mysterud

Mysterud, A. 1998: Large male territories in a low-density population of roe deer *Capreolus capreolus* with small female home ranges. - Wildl. Biol. 4: 231-235.

Two hypotheses regarding roe deer spacing in low-density areas during the breeding season are: 1) that male territory size is equal to that of the female home range size or 2) that male territory size is larger than the female home range. I tested the two hypotheses using data on the home range sizes of nine female, and the territory sizes of 12 male roe deer radio-tracked during the summers of 1994-1996 in the Lier valley, southern Norway. There was no support for hypothesis 1, as male territory size was 1.5-1.9 times larger than female home ranges after correcting for altitude. Contradictory results in the literature regarding the effect of density on male roe deer territory size suggest that density alone does not satisfactorily predict roe deer spacing. I present the female dispersion hypothesis which presumes that as the area occupied by females decreases (due to high resource levels), the cost-effectiveness of male territoriality increases. Thus, the territory size of roe deer males, relative to female home range size, is expected to be largest when females are divided into local spatial units and female home range is relatively small. Comparative observations in two low-density populations seem to support this hypothesis.

Key words: Capreolus capreolus, home range, mating system, roe deer, social organisation, territoriality

Atle Mysterud, Department of Biology, Division of Zoology, University of Oslo, P.O. Box 1050 Blindern, N-0316 Oslo, Norway - e-mail: atle.mysterud@bio.uio.no

Received 21 July 1997, accepted 13 March 1998

Associate Editor: Jean-Michel Gaillard

In mammals, female reproductive success is generally limited by access to resources, whereas male reproductive success is limited by access to females (Trivers 1972, Davies 1991). The spatial distribution of females, therefore, generally reflects spatial and temporal resource distribution, whereas distribution of males during the breeding season is influenced more by the distribution of receptive females (e.g. Ostfeld 1985, Ims 1987, 1988). Spacing systems may differ between populations of the same species according to differences in density, and female home range size and spatial distribution (Clutton-Brock 1989, Davies 1991).

Female roe deer *Capreolus capreolus* live solitarily in undefended areas during the breeding season, whereas male roe deer have been reported to be territorial over its entire geographical range at highly varying densities (Bramley 1970, Strandgaard 1972, Ellenberg 1978, Cederlund 1983, Bjar, Selås, Lund & Hjeljord 1991, Bideau, Gerard, Vincent & Maublanc 1993, Andersen, Linnell & Aanes 1995, Vincent, Bideau, Hewison & Angibault 1995, Johansson 1996). Territoriality probably represents a mating strategy (Wahlström 1994, Andersen et al. 1995, Cederlund & Liberg 1995, Johansson 1996), although no alternative mating strategy to territoriality has been reported.

The effect of density on the territory size of roe deer males is debated. Two recent studies showed no change in territory size as density increased from medium to high (Andersen et al. 1995, Johansson 1996), whereas two others suggested that male territory size, but not female home ranges, decrease with increasing density (Ellenberg 1978, Vincent et al. 1995). Ellenberg (1978), however, studied a fenced, artificially fed population without the aid of radiotelemetry, and Vincent et al. (1995) reported annual range sizes that include also the non-territorial season. Possible confounding effects of habitat were not addressed.

Data on the spacing system of roe deer in low-density populations (<5 deer/100 ha) are limited to the study by Cederlund (1983) at Grimsö, Sweden, where territory and home range sizes for both sexes were about 95 ha. Hence, there is a need for more information about roe deer spacing in low-density areas. I therefore tested whether 1) male territories are as large as female home ranges or whether 2) male territories are larger than female home ranges in a low-density population (3-5 deer/100 ha; Mysterud 1993) in Norway. I also discuss two further hypotheses that may be necessary to predict roe deer spacing systems in low-density populations. One of these incorporates female dispersion which so far has been overlooked in the literature on roe deer spacing systems.

Study area

The study area is located in the Lier valley, Buskerud county in southern Norway (between 59°45'- 60°00'N and 10°05'-10°20'E) and has been described in detail by Mysterud & Østbye (1995a,b). The area is forested and situated within the boreonemoral region (Abrahamsen, Jacobsen, Kalliola, Dahl, Wilborg & Påhlsson 1977), but at lower altitudes forest stands are interspersed with small agricultural fields. The topography is hilly, rising from Lake Holsfjorden at 63 m a.s.l. to over 500 m 1.5-2.5 km from the lake. Forest appraisal maps of the area clearly indicate that productivity declines with altitude. Roe deer males defend their territories from April/May through August (A. Mysterud, unpubl. data).

Material and methods

Adult roe deer (≥2 year old) were captured in box traps or nets during February-March in 1994-1996, and fitted with radio-collars (Televilt Int. AB transmitters, TXE-3). Deer were tracked during three consecutive summers: 1994 (two females and three males), 1995 (five females and five males) and 1996 (two females and four males), though each deer was followed only one summer. One of two collared 2-year-old bucks was non-territorial with a range of 670 ha and was excluded from the analysis. This individual was therefore followed one more year, and its range as a 3-year-old was included. Radio-fixes were obtained at an average interval of 18 hours (starting at 10:00) during 1-25 July (one male and one female was followed in June 1995, but range sizes were equal between June and July 1995; A. Mysterud, unpubl. data). The starting point of the tracking route (lasting 2-8 hours) was chosen at random so that each deer was triangulated at all hours to avoid biases.

Range sizes were estimated using the Minimum Convex Polygon method (MCP-100) (Mohr 1947), peeled MCP (MCP-95), excluding 5% of the observations most peripheral to the harmonic mean (Schoener 1981) and the Kernel method (Worton 1989) with the 90% isoline. The RANGES IVm software package was used for all calculations. The choice of methods was guided by Andreassen, Ims, Stenseth & Yoccoz (1993).

The two hypotheses regarding the effect of sex on differences in range size were tested. The MCP-95 home range estimates were used as the response variable, since MCP-95 shows better stability with an increasing number of fixes than the MCP-100 (A. Mysterud, unpubl. data). The MCP-95 estimates were close in size to the 90% Kernel estimates (see below). Thirty fixes were used since this has been a recommended standard (Kenward 1987). I simultaneously controlled for possible effects of year (e.g. density, temperature, productivity) and for altitude (see study area description).

Results

Male territories were larger than female home ranges (ANCOVA, N = 21, $r^2 = 0.756$, F = 5.502, df = 1, P = 0.044). Range size increased with altitude (F = 15.851, df = 1, P = 0.003), but there were no differences in range size between years (F = 1.096, df = 2, P = 0.375). None of the interactions were significant (sex*altitude: F = 0.383, df = 1, P = 0.551; sex*year: F = 0.415, df = 2, P = 0.672; altitude*year: F = 1.154, df = 2, P = 0.358; sex*altitude*year: F = 0.406, df = 2, P = 0.678). Observations of adult males chasing younger males justify that male home ranges are called territories; the territories of the 12 territorial males averaged 105.4 ha (range: 41.4 - 292.3 ha), whereas female home ranges averaged 49.5 ha (N = 9, range: 5.6 - 119.8 ha) as measured by MCP-95. Range sizes for males and females were 60.7 ha (N = 7) and 32.0 ha (N = 7; ratio 1.9) at low elevations (below 250 m a.s.l.), and 167.8 (N = 5) and 110.8 (N = 2; ratio 1.5) at high elevations (above 250 m a.s.l.), respectively. Average male and female range sizes were 138.8 and 85.6 ha using MCP-100, and 119.9 ha and 55.7 ha with the Kernel 90% estimate, respectively.

Overlap between adjacent buck territories (N = 3) measured by MCP-95 averaged 0.1% (0-0.3%). Only in one case was a female rut excursion recorded (*sensu* Andersen et al. 1995, Cederlund & Liberg 1995, Johansson 1996). This female was recorded 5.9 km outside her regular home range on 13 July, 1994 (on 11 June and 13 August the same female also moved to the same main area, A. Mysterud, unpubl. data). She left at night and returned the next night.

Discussion

The home range sizes of female roe deer reported in my study are fairly close to those reported from a study in a medium-high density area holding 10 deer/100 ha further south in Norway (Bjar et al. 1991). Female range size varies little with density (Ellenberg 1978, Vincent et al. 1995, Tufto, Andersen & Linnell 1996), and mainly reflects differences in range quality (Bobek 1977, Wahlström & Kjellander 1995, Tufto et al. 1996). Territory size in my study was stable between years, indicating a stable density during the study period.

The hypothesis that male territories are equal in size to female home ranges during the breeding season in low-density areas (Cederlund 1983) was not supported. But the results of the present study supported the hypothesis that males defend territories which are larger than female home ranges in a low-density population. However, the magnitude of the difference was surprisingly large (ratio up to 1.9 compared to 1.5 reported by Vincent et al. (1995) at a density of 5-7 deer/100 ha), especially when compared to the ratio of 1.0 in the Grimsö study in Sweden (Cederlund 1983) which reported a density of 3-4 deer/100 ha comparable to the 3-5 deer/100 ha in Lier, Norway (Mysterud 1993). Both Grimsö and Lier lie in forested areas. I therefore suggest that two different, though not mutually exclusive, hypotheses may be used to predict male spacing at low density: 1) the male density hypothesis (Johansson 1996) and 2) the female dispersion hypothesis (Clutton-Brock 1989).

The male density hypothesis

The male density hypothesis states that male range size increases when male density, not density *per se*, decreases (Johansson 1996). The sex-ratio may differ between populations due to different levels of (i) male-biased fawn predation by red fox *Vulpes vulpes* (Aanes & Andersen 1996) or (ii) selective buck hunting by humans. However, it seems that this hypothesis alone cannot explain the difference in spacing system observed in the study areas at Grimsö and Lier. In both the Grimsö study area in Sweden (Cederlund 1983) and the Lier valley in Norway (this study) foxes were present during the study (Lindström, Andrén, Angelstam, Cederlund, Hörnfeldt, Jäderberg, Lemnell, Martinsson, Sköld & Swenson 1994, A. Mysterud, pers. obs.). Furthermore, due to similar hunting traditions in Sweden and Norway (the hunting season for males is one month longer than the hunting season for females in both countries), there is no reason to believe that differences in hunting pressure are large enough to produce different sex ratios in the two areas.

The female dispersion hypothesis

The female dispersion hypothesis assumes that the cost-effectiveness of male territoriality increases as areas occupied by females decrease due to higher resource levels (Clutton-Brock 1989). Some evidence supporting this hypothesis can be found in other ungulates:

a) Within Reduncinae (kobs *Kobus kob*, lechwe

Kobus leche, waterbuck *Kobus defassa* and reedbuck *Redunca arundinum*) the (mating) territory size of males is greatest when female populations are divided into local spatial subunits, and female range size is relatively small (Clutton-Brock 1989);

b) Territoriality has been observed as an alternative mating strategy in some Spanish populations of red deer *Cervus elaphus* (Carranza, Alvarez & Redondo 1990); it is regarded as more costly than female defence (in terms of aggressive encounters) and is correlated with patches of high-quality food (Carranza, Fernandez-Llario & Gomendio 1996);

c) Similarly, in pronghorn *Antilocapra americana*, male territoriality is correlated with high resource density (Maher 1994).

Observations of different spacing systems of roe deer at low density in the Lier and Grimsö study areas also seem to support this hypothesis; female home ranges at Grimsö (Cederlund 1983) were about twice the average size of those in the Lier valley. Spatial clumping of females as reported within the Reduncinae (see a) above) is likely to occur in roe deer populations held below carrying capacity, since dispersal of females is small at low population densities (Wahlström & Liberg 1995) and since daughters settle on home ranges adjacent to their mothers' home ranges (Bjar et al. 1991). I therefore suggest that the female dispersion hypothesis, the combination of low population density (measure of intruders, costs) and small, clumped female home ranges (due to high resource abundance, benefits) can explain the spacing differences in male roe deer observed between this and the Grimsö study.

One underlying assumption of both the male density and the female dispersion hypotheses is that the territory holder obtains benefits through large territory size. However, Johansson (1996) found no increase in reproductive success with increasing territory size in a high-density population in Sweden. This does not, however, give sufficient reason to dismiss the two hypotheses, since the negative relationship was probably dependent on one outlier (O. Liberg, pers. comm.), and the study was carried out in a high-density population. Although the sample size in my study was small, my results suggest that large territories are an effective strategy in Lier, since only one female (11.1%, N = 9) made a rut excursion (presumably to visit another male) compared to 30-50% of females in high-density populations (Andersen et al. 1995, Johansson 1996). Other hypotheses must be advanced to fully explain the stable territory size and increasing overlaps of territories when population density increases from medium to high (10-40 deer/100 ha, Andersen et al. 1995, 10-25 deer/100 ha, Johansson 1996). I suggest that changes in territory size and changes in overlap occur in a sequence: male territory size decreases as population density increases from low to medium (depending on female range size/dispersion), whereas during increases from medium to high density, the territory size remains stable but the degree of territory overlap increases.

Acknowledgements - I thank Rolf Anker Ims, Ivar Mysterud, Carole Toïgo, Jerry Thomas Warren, Eivind Østbye and one anonymous referee for valuable comments on an earlier version of the manuscript and Tom Einar Øverby for help during capturing of animals. The study was supported by grants from the Norwegian Council for Research (NFR), and funding for field work was provided by Viltfondet centrally (Directorate for Nature Management) and from the County Officers in Buskerud, Hedmark, Oppland, Telemark and Vestfold counties.

References

Aanes, R. & Andersen, R. 1996: The effects of sex, time of birth, and habitat on the vulnerability of roe deer fawns to red fox predation. - Canadian Journal of Zoology 74: 1857-1865.

Abrahamsen, J., Jacobsen, N.K., Kalliola, R., Dahl, E., Wilborg, L. & Påhlsson, L. 1977: Naturgeografisk regioninndeling av Norden. - Nordiska Utredningar Series B 34: 1-135. (In Norwegian).

Andersen, R., Linnell, J.D.C. & Aanes, R. 1995: Rådyr i kulturlandskapet. (In Norwegian with English summary: Roe deer in a cultural landscape). - Fagrapport NINA 010, 80 pp.

Andreassen, H.P., Ims, R.A., Stenseth, N.C. & Yoccoz, N.G. 1993: Investigating space use by means of radiotelemetry and other methods: a methodological guide. - In: Stenseth, N.C. & Ims, R.A. (Eds.); The biology of lemmings. The Linnean Society of London, London, pp. 589-618.

Bideau, E., Gerard, J.F., Vincent, J.P. & Maublanc, M.L. 1993: Effects of age and sex on space occupation by European roe deer. - Journal of Mammalogy 74: 745-751.

Bjar, G., Selås, V., Lund, L.O. & Hjeljord, O. 1991: Movements and home range dynamics of roe deer, Capreolus capreolus L., in southeastern Norway. - Fauna norvegica Series A 12: 12-18.

Bobek, B. 1977: Summer food as the factor limiting roe deer population size. - Nature 268: 47-49.

Bramley, P.S. 1970: Territoriality and reproductive behaviour of roe deer. - Journal of Reproductive Fertility, Supplement 11: 43-70.

Carranza, J., Alvarez, F. & Redondo, T. 1990: Territoriality as a mating strategy in red deer. - Animal Behaviour 40: 79-88.

Carranza, J., Fernandez-Llario, P. & Gomendio, M. 1996: Correlates of territoriality in rutting red deer. - Ethology 102: 793-805.

Cederlund, G. 1983: Home range dynamics and habitat selection by roe deer in a boreal area in central Sweden. - Acta Theriologica 28: 443-460.

Cederlund, G. & Liberg, O. 1995: Rådjuret. Viltet, ekologin och jakten. - Svenska Jägareforbundet, Solna, 301 pp. (In Swedish).

Clutton-Brock, T.H. 1989: Mammalian mating systems. - Proceedings of the Royal Society of London Series B 236: 339-372.

Davies, N.B. 1991: Mating systems. - In: Krebs, J.R. & Davies, N.B. (Eds.); Behavioural Ecology, an evolutionary approach. Blackwell Scientific publication, London, pp. 263-294.

Ellenberg, H. 1978: Zur Populationsökologie des Rehes (Capreolus capreolus L., Cervidae) in Mitteleuropa. (In German with English summary: On the population ecology of roe deer (Capreolus capreolus L., Cervidae) in central Europe). - Spixiana, Supplement 2: 1-211.

Ims, R.A. 1987: Responses in the spatial organization and behaviour to manipulations of the food resource in the vole Cletrionomys rufocanus. - Journal of Animal Ecology 56: 585-596.

Ims, R.A. 1988: Spatial clumping of sexually receptive females induces space sharing among male voles. - Nature 335: 541-543.

Johansson, A. 1996: Territorial dynamics and marking behaviour in male roe deer. - PhD thesis, University of Stockholm, 44 pp.

Kenward, R. 1987: Wildlife radio tagging. - Academic Press, London.

Lindström, E.R., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P-A., Martinsson, B., Sköld, K. & Swenson, J. 1994: Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. - Ecology 75: 1042-1049.

Maher, C.R. 1994: Pronghorn male spatial organization: population differences in degree of nonterritoriality. - Canadian Journal of Zoology 72: 455-464.

Mohr, C.O. 1947: Table of equivalent populations of North American small mammals. - American Midland Naturalist 37: 223-249.

Mysterud, A. 1993: Rådyrets (Capreolus capreolus) liggeplasser og leieatferd om vinteren. - M.Sc. thesis, University of Oslo, 93 pp. (In Norwegian).

Mysterud, A. & Østbye, E. 1995a: Bed-site selection by European roe deer (Capreolus capreolus) in southeastern Norway during winter. - Canadian Journal of Zoology 73: 924-932.

Mysterud, A. & Østbye, E. 1995b: Roe deer Capreolus capreolus feeding on yew Taxus baccata in relation to bilberry Vaccinium myrtillus density and snow depth. - Wildlife Biology 1: 249-253.

Ostfeld, R.S. 1985: Limiting resources and territoriality in microtine rodents. - American Naturalist 126: 1-15.

Schoener, T.W. 1981: An empirically based estimate of home range. - Theoretical Population Biology 20: 281-325.

Strandgaard, H. 1972: The roe deer (Capreolus capreolus) population at Kalø and the factors regulating its size. - Danish Review of Game Biology 7 (1): 1-205.

Trivers, R.L. 1972: Parental investment and sexual selection. - In: Campbell, B. (Ed.); Sexual selection and the descent of man. Aldine Press, Chicago, pp. 136-179.

Tufto, J., Andersen, R. & Linnell, J.D.C. 1996: Habitat use and ecological correlates of home range size in a small cervid: the roe deer. - Journal of Animal Ecology 65: 715-724.

Vincent, J.P., Bideau, E., Hewison, A.J.M. & Angibault, J.M. 1995: The influence of increasing density on body weight, kid production, home range and winter grouping in roe deer (Capreolus capreolus). - Journal of Zoology 236: 371-382.

Wahlström, L.K. 1994: The significance of male-male aggression for yearling dispersal in roe deer (Capreolus capreolus). - Behavioral Ecology and Sociobiology 35: 409-412.

Wahlström, L.K. & Kjellander, P. 1995: Ideal free distribution and natal dispersal in female roe deer. - Oecologia 103: 302-308.

Wahlström, L.K. & Liberg, O. 1995: Patterns of dispersal and seasonal migration in roe deer (Capreolus capreolus). - Journal of Zoology 235: 455-467.

Worton, B.J. 1989: Kernel methods for estimating the utilization distribution in home-range studies. - Ecology 70: 164-168.