Paternity and mating system in wolverines Gulo gulo

Authors: Hedmark, Eva, Persson, Jens, Segerström, Peter, Landa, Arild, and Ellegren, Hans

Source: Wildlife Biology, 13(sp2) : 13-30

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396(2007)13[13:PAMSIW]2.0.CO;2

Paternity and mating system in wolverines *Gulo gulo*

Eva Hedmark, Jens Persson, Peter Segerström, Arild Landa & Hans Ellegren

Hedmark, E., Persson, J., Segerström, P., Landa, A. & Ellegren, H. 2007: Paternity and mating system in wolverines *Gulo gulo*. - Wildl. Biol. 13 (Suppl. 2): 13-30.

Knowledge of the wolverine *Gulo gulo* mating system is limited. In this study, we use 20 microsatellite loci for paternity testing in 145 wolverine offspring with known mothers. Samples were collected during > 10 years in two Scandinavian populations, mainly in connection with radio-telemetry studies and as part of long-term population monitoring. In total, 51% of the offspring were assigned a father. Our results demonstrate that the wolverine exhibits a polygamous mating system as some males were shown to produce offspring with more than one female in a single year. Females often reproduced with the same male in subsequent breeding years, but sometimes changed their partner, potentially as a consequence of a change in the territory-holding male in the area. In the majority of litters, siblings were unambiguously assigned the same father, indicating that multiple paternity is rare. Of 23 breeding pairs, for which telemetry data were available, 20 had overlapping home ranges, suggesting that pair formation generally is consistent with the territories held by wolverine males and females.

Key words: Gulo gulo, microsatellite, multiple paternity, parentage analysis

Eva Hedmark & Hans Ellegren, Department of Evolutionary Biology, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden - e-mail addresses: eva.hedmark@gmail.com (Eva Hedmark); hans.ellegren@ebc.uu.se (Hans Ellegren)
Jens Persson & Peter Segerström, Grimsö Research Station, Department of Conservation Biology, Swedish University of Agricultural Sciences, SE-730 91 Riddarhyttan, Sweden - e-mail addresses: jens.persson@nvb.slu.se (Jens Persson); peter@solbritt.se (Peter Segerström)
Arild Landa, Norwegian Institute for Nature Research, Tungasletta 2, N-7485 Trondheim, Norway - e-mail: arild.landa@nina.no

Corresponding author: Jens Persson

The wolverine *Gulo gulo* is a medium-sized, solitary carnivore occurring at low densities in remote areas of northern tundra and taiga in Eurasia and North America. Wolverines exhibit intra-sexual territoriality and males usually have large territories that overlap those of a few females (Magoun 1985, Banci 1994). The mating system has been suggested to be polygamous based on field observations (Rausch & Pearson 1972), but our knowledge is limited and genetic techniques have not been applied for analyses of parentage or other close relationships.

Previously, wolverines were widely distributed in Scandinavia, however, at the beginning of the 20th century the population declined drastically due to human persecution (Landa et al. 2000). The species received legal protection in 1969 in Sweden and during 1973-1983 in Norway, and the population has since then started to recover slowly. According to records of active natal dens (Landa et al. 1998), the current Scandinavian population size amounts to about 330 individuals in Norway (http://nidaros.nina.no/overvaking/jerv/Nystatus30112005.pdf) and

approximately 480 individuals in Sweden (http://www.naturvardsverket.se/dokument/natur/rovdjur/rovdok/varfinns.htm). The majority of the wolverines are found in the mountain range along the border of Sweden and Norway, but a small subpopulation (~ 80 individuals) is also present in central parts of southern Norway. Genetic studies have revealed low levels of microsatellite diversity in Scandinavian wolverines (Walker et al. 2001), and that the subpopulation in southern Norway is differentiated from the mountain-range population (Walker et al. 2001, Flagstad et al. 2004). Moreover, since 2001 non-invasive genetic techniques are used to aid in population monitoring (Flagstad et al. 2004), with genetic data being directly implemented in national management programmes in Sweden and Norway.

For management of threatened populations to be effective, it must be based on thorough knowledge of the biology of the species. Understanding the mating system can be important as it influences the ability of a population to maintain genetic diversity. With information on parentage and individual mating success, the effective population size may be assessed. In conservation this is essential as the genetic diversity in small populations decreases at a rate dependent on the effective population size. Genetic parentage and relatedness analysis have proven to be useful in studies of social organisation and mating system in wild populations (e.g. Moritz et al. 1997, Girman et al. 1997, Garnier et al. 2001, Constable et al. 2001, Kovach & Powell 2003, Huck et al. 2005). However, the low level of genetic diversity observed in the Scandinavian wolverine population means that the power and resolution of such analysis may be lower than for other species. On the other hand, the fact that a large number of mother-offspring pairs are known from telemetry studies acts in the opposite direction, since the ability to find the biological father is facilitated when maternal genotypes are specified (Marshall et al. 1998). To study the mating system of Scandinavian wolverines, we combine genetic analysis of 20 microsatellite loci in more than 300 individuals, with telemetry data available from 181 of these animals.

Material and methods

Study areas and samples

Samples were from two study areas, one in northern Sweden located in and around Sarek National Park (Kvikkjokk; 67°00'N, 17°40'E) and one around the Snøhetta plateau (62°00'N, 10°00'E) in central southern Norway (Fig. 1). Both areas are characterised by deep valleys, high alpine plateaus and peaks up to 2,000 m a.s.l. Based on the number of recorded natal dens (*cf*. Landa et al. 1998), the approximate density of wolverines has been estimated at 1.4/100 km^2 in the area of Sarek National Park (Persson 2003).

In northern Sweden, small tissue biopsies for DNA analysis were taken from immobilised animals that were captured for radio-marking in a long-term study of wolverine ecology during 1993-2004 (e.g. Persson et al. 2003). In this study, animals were equipped with implanted radio-transmitters with mortality sensors. Movements of marked animals were monitored by means of traditional radio-tracking from the air and the ground. We sampled 111 offspring of radio-marked females at the age of 2-3 months at rendezvous sites (sites where offspring were left while the female foraged). These offspring were reared in 63 litters by 37 different females, which also were sampled for tissue. Five were litters with three offspring, 38 with two offspring and 20 with a single offspring. In addition, 29 male wolverines of unknown age and relation to other individuals were sampled for tissue. Adult individuals were either darted from helicopter, or in some cases for females, captured at rendezvous sites following snow-tracking.

From the southern Norway population, tissue from 18 offspring was sampled during radio-telemetry and 16 were obtained from offspring legally killed together with their mothers in a programme for carnivore control in conflict areas. The 34 offspring, sampled during 2001-2004, were reared in 16 litters by 15 different females. Three were litters with three offspring, 12 with two offspring and one with a single offspring. All mothers were also sampled (in one case with a faecal sample, otherwise with tissue). In addition, a vast number of additional wolverine samples (33 tissue and approximately 1,200 faecal samples) were collected in southern Norway during 2000-2004 as part of a national population monitoring programme, based on non-invasive sampling (Flagstad et al. 2004, Flagstad et al. 2005). These turned out to represent 80 males, 76 females and nine individuals of unknown sex.

Laboratory analysis

DNA from tissue was extracted using a phenol: chloroform protocol (Sambrook et al. 1989) and

Figure 1. The two study populations are indicated by circles. Hatched areas represent the current wolverine distribution in the Nordic countries.

was used for genotyping with 20 microsatellite markers (Table 1). PCR was performed in 10 µl reactions containing 1 × AmpliTaq Buffer, 1.5-3.0 mM $MgCl_2$, 0.2 mM of each dNTP, 3.2 pmol of each primer, 0.3 U of AmpliTaq DNA polymerase (Applied Biosystems) and 20 ng DNA. Initial denaturation at 94°C for three minutes was followed by 32-34 cycles of amplifications with 94°C for 30 seconds, 52-58°C for 30 seconds and 72°C for one minute, and a final extension at 72°C for 10 minutes. For Lut604 a touch-down program was used; three minutes at 94°C, 20 touch-down cycles with 30 seconds at 94°C, 30 seconds at 60°C decreasing 0.5°C each cycle, and one minute at 72°C, followed by 23 cycles of 30 seconds at 94°C, 30 seconds at 50°C, and 72°C for one minute. Prior to 2003, PCR products were run on an ABI 377 instrument (Applied Biosystems, Foster City, CA, USA). From 2003

Table 1. Number of alleles (A) and observed and expected heterozygosity (H_{obs} and H_{exp}) in the studied wolverine populations.

	Northern Sweden			Southern Norway			
Marker	A	H_{obs}	H_{exp}	A	H_{obs}	H_{exp}	Reference
Tt-4	3	0.22	0.25	2	0.07	0.15	Davis & Strobeck 1998
Gg-7	2	0.59	0.50	3	0.60	0.63	Davis & Strobeck 1998
Ggu10	4	0.54	0.55	4	0.41	0.49	Walker et al. 2001
Ggu14	4	0.49	0.56	3	0.58	0.58	Walker et al. 2001
Ggu25	3	0.61	0.56	3	0.59	0.60	Walker et al. 2001
Ggu42	3	0.33	0.34	3	0.27	0.28	Walker et al. 2001
Mvis057	4	0.55	0.48	4	0.42	0.43	O'Connell et al. 1996
Mvis072	3	0.65	0.63	3	0.59	0.60	O'Connell et al. 1996
Mvis075	4	0.74	0.71	4	0.65	0.68	O'Connell et al. 1996
Gg101B	3	0.42	0.40	3	0.41	0.45	Duffy et al. 1998
Gg216	5	0.70	0.64	5	0.52	0.61	Duffy et al. 1998
Gg234	4	0.52	0.59	4	0.60	0.57	Duffy et al. 1998
Gg238	6	0.61	0.63	6	0.10	0.55	Duffy et al. 1998
Gg443	3	0.36	0.41	3	0.33	0.38	Walker et al. 2001
Gg452	4	0.57	0.58	4	0.48	0.51	Walker et al. 2001
Gg454	5	0.74	0.63	5	0.62	0.66	Walker et al. 2001
Gg465	3	0.64	0.57	3	0.61	0.58	Walker et al. 2001
Gg470	2	0.32	0.31	2	0.36	0.49	Walker et al. 2001
Gg471	2	0.23	0.31	2	0.42	0.50	Walker et al. 2001
Lut604	2	0.49	0.50	2	0.42	0.45	Dallas & Piertney 1998
Mean	3.45	0.52	0.51	3.40	0.45	0.51	-

and onwards all genotyping were performed using a MegaBACE 1000 capillary instrument (Amersham Biosciences). Consistency in allele scoring on the different instruments was secured through careful calibration where several wolverine samples were analysed on both machines.

In all microsatellite analyses from faecal DNA we applied a multiple-tube approach requiring a minimum of three unambiguous amplification results to accept a homozygous genotype. Moreover, both alleles had to be observed at least twice for a heterozygous genotype. Details on the procedure of DNA extraction, microsatellite genotyping, interpretation and molecular sexing from wolverine faecal samples are provided in Hedmark et al. (2004) and Flagstad et al. (2004).

Population genetic analysis

Allele frequencies were calculated separately for each population using GIMLET 1.3.1 (Valière 2002). In northern Sweden, allele frequencies were estimated from individuals sampled as adults (N = 69) to avoid biases towards related individuals. In southern Norway, the estimate was based on all individuals except the 34 known offspring. We tested for departure from Hardy-Weinberg equilibrium (HWE) and for linkage disequilibrium using the GENEPOP 3.4 software (Raymond & Rousset 1995). Sequential Bonferroni correction (Rice 1989) was applied for multiple tests.

Paternity analysis

Paternity assignments were based on paternity tests performed in CERVUS 2.0 (Marshall et al. 1998) and on relatedness estimates between pairs of individuals calculated in KINSHIP (Goodnight & Queller 1999). CERVUS uses the principles of Mendelian inheritance and the population allele frequencies to determine which male, from a pool of candidates, is the most likely father. The program uses simulations to define a critical value of the log-likelihood (LOD) difference between the two most likely candidates. However, since the accuracy of these critical values relies on the assumption that no relatives are present, which is likely to be the case in our populations, we applied a number of other criteria to assign paternity. Each criterion is explained in detail below.

Parameters in CERVUS were specified to allow a 1% genotyping error rate, and varying proportions of males sampled in different areas and during different time periods (depending on sampling). The number of animals captured each year in northern Sweden increased progressively during the course of the study and the proportion of sampled males was therefore higher in later years. Also, the central parts of our study area in northern Sweden

were more intensively monitored. Accordingly, offspring in northern Sweden were divided into four groups: core area 1993-1998, core area 1999-2004, periphery 1993-1998 and periphery 1999-2004. For these groups we estimated that 55, 85, 25 and 60% of the male population was sampled, respectively. These estimates were obtained by assuming that all parts of the study area in northern Sweden were inhabited by wolverines and that male home ranges (100% minimum convex polygon; MCP) were non-overlapping. The study area (core and periphery, respectively) was divided by the average size of a male home range in northern Sweden (400 km^2; J. Persson, unpubl. data) to obtain the number of males expected in each area. The number of sampled males present in each area a given year (as known from telemetry) was divided by the number of males expected to be present. The obtained proportions were then averaged over the years within each of the two time periods. In southern Norway, the estimated proportion of males sampled (80%) was based on population size estimates (Flagstad et al. 2005).

In paternity tests, the mother was always given, and all males sampled by either tissue or faeces in the respective population were considered as potential candidates, with the exception of males known to have died before mating and known male siblings of the analysed offspring. Moreover, as most wolverine males do not reach sexual maturity before two years of age (Rausch & Pearson 1972, Banci & Harestad 1988), males of known age were not considered as possible fathers until they were in their third year of life. Also in CERVUS, allele frequencies were specified to avoid biases towards related individuals. Thus, allele frequencies used for northern Sweden were based on individuals sampled as adults (N = 69), and for southern Norway on all sampled individuals except the 34 known offspring.

A genetic relatedness index, r, between pairs of individuals was calculated using KINSHIP 1.3.1 (Goodnight & Queller 1999), based on the method of Queller & Goodnight (1989). The index is calculated from population allele frequencies and assesses the proportion of alleles between two individuals that are identical by decent. The r-value ranges from -1 to 1, and should be 0.5 for first order relatives (i.e. parent-offspring pairs and full siblings), 0.25 for second order relatives and zero for unrelated pairs. Given the low genetic diversity of Scandinavian wolverines and the relatively limited number of markers available, r is likely to show a wide distribution around the expected value. Based on the observed allele frequencies from each population, we generated 1,000 pairs each of unrelated individuals, half siblings and parent-offspring to obtain the expected distributions. The distribution of r for parent-offspring pairs was also obtained for known mother-offspring pairs in northern Sweden and southern Norway, respectively.

Paternity assignment

To assign a male as the father of offspring, we applied four criteria: 1) the LOD-score obtained in CERVUS had to be 3.0 or more; 2) the r-value between the male and the offspring had to exceed the cut-off value at which 95% of 1000 simulated parent-offspring pairs fell; 3) no more than one mismatching allele was accepted among mother-offspring-father trios (allowing one mismatching allele can be justified by the fact that genotyping errors are difficult to completely avoid, especially in analysis of faecal DNA); 4) a male was not assigned paternity if his r-value to the mother exceeded a cut-off value at which 95% of 1000 simulated unrelated pairs fell. The last criterion was included to reduce the risk that a (unknown) brother or uncle, or other male relative, would be incorrectly assigned paternity. Moreover, if more than one male fulfilled all criteria the one with the highest LOD-score was assigned paternity, unless for a few exceptions where telemetry data and/or relatedness analysis suggested that the male with the second highest LOD-score was more likely. In such cases paternity was not assigned; these cases are described in detail in Appendix III.

Results

Average heterozygosity across all loci was 0.52 and 0.45 for northern Sweden and southern Norway, respectively (see Table 1). The number of alleles per locus ranged within 2-6 in both populations with a mean of 3.45 in northern Sweden and 3.40 in southern Norway (see Table 1). This level of genetic variation is comparable to what has previously been observed among Scandinavian wolverines (Walker at al. 2001, Flagstad et al. 2004), but is lower compared to wolverines in several regions of North America (Kyle & Strobeck 2001, 2002). In northern Sweden, all loci were unlinked and in HWE. In southern Norway, one locus, Mvis075, deviated significantly from HWE and 21 of 190

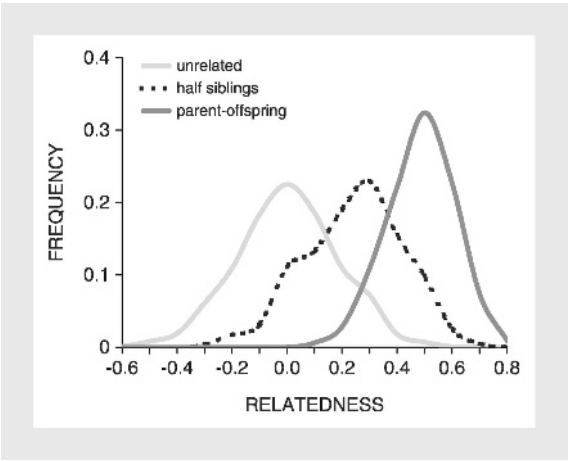

Figure 2. Distribution of relatedness values for 1000 simulated pairs of unrelated individuals, half siblings and parent-offspring generated based on observed allele frequencies in northern Sweden. The allele frequencies observed in the southern Norway population provide a similar distribution (graph not shown).

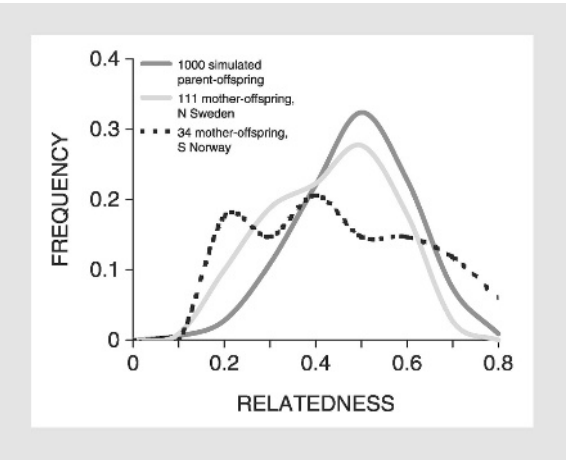

Figure 3. Distribution of relatedness values for 1000 simulated parent-offspring pairs and for known mother-offspring pairs in northern Sweden (N = 111) and southern Norway (N = 34).

pairs of loci appeared to be linked. The non-random association observed in Norway was probably caused by chance events typical of small populations and/or recent admixture.

The range of simulated r-values within each relatedness category (unrelated, half siblings and parent-offspring) overlapped with that of other categories (Fig. 2), reducing the ability to distinguish between different categories. Nevertheless, since 95% of parent-offspring pairs fell above an r-value of 0.27-0.28 in the two populations and 95% of unrelated individuals fell below 0.31, there was potential to distinguish between these categories. The distribution of observed relatedness values for known mother-offspring pairs in northern Sweden was similar to that obtained from simulations, although slightly skewed towards lower values (Fig. 3). The distribution obtained for the limited number of mother-offspring pairs in southern Norway (N = 34) was wide and irregular (see Fig. 3).

Paternity assignments

With the set of 20 microsatellites and the allele frequencies observed in each population, the total exclusionary power for the second parent was 0.9981 in northern Sweden and 0.9976 in southern Norway. Paternity was resolved for 74 of the 145 offspring (51%; Table 2). For 50 of these offspring only one male fulfilled the assignment criteria. For the remaining 24, the male that showed the highest LOD-score among two or more that fulfilled the criteria was assigned. In northern Sweden paternity was resolved in 57 cases with 14 different males being assigned as fathers (Appendix I). These 57 offspring were reared in 36 litters by 23 different females. Eight of the 14 assigned males reproduced with more than one female, six males with two females and two with three. There were six occasions where one male reproduced with two different females in the same year. In southern Norway, paternity could be resolved for 17 offspring of seven different females (see Appendix I). All southern Norway females reproduced with different males. The only female for which two litters were sampled reproduced with the same male.

Telemetry data revealed that breeding male and female home ranges overlapped in 20 out of 23 cases, with home range borders located within 2-5 km from each other in the remaining three cases. The home ranges of males breeding with different females generally overlapped with each of the females' ranges (Fig. 4).

Females often reproduced with the same male in subsequent breeding years. Only two out of 11 females that produced more than one sampled litter in which paternity was resolved bred with two different males. However, if data from females with at least one litter with resolved paternity and at least one with unresolved paternity was also included, and assuming that the father in the latter case was different from the former, eight out of 13 females bred with different males (Appendix II). Two females (J9647 and J9651) were shown to breed with a new male although their previous breeding partner was still alive according to telemetry. Moreover, in one of these cases the

Table 2. Summary of paternity assignments. Data is shown separately for each temporal/spatial group in northern Sweden. Dubious cases are explained in detail in Appendix III.

Group	Total number of offspring	Number of assigned paternities (%)	Number of offspring for which all candidates could be excluded (%)	Dubious cases (%)
Northern Sweden, core 1993-1998	36	7 (19)	28 (78)	1 (3)
Northern Sweden, periphery 1993-1998	5	0 (0)	5 (100)	0 (0)
Northern Sweden, core 1999-2004	55	39 (71)	12 (22)	4 (7)
Northern Sweden, periphery 1999-2004	15	11 (73)	2 (14)	2 (14)
Southern Norway	34	17 (50)	11 (32)	6 (18)

first male still had a home range that partly overlapped with that of the female.

Multiple paternity

A single male genotype could in all cases explain the paternal alleles observed among siblings within litters. However, the possibility to detect multiple paternity by counting paternal alleles was limited in our study as there were only eight litters with three offspring. Moreover, the number of alleles at each locus was limited. However, a possible case of multiple paternity was indicated from a litter with incomplete paternity assignment. In this litter, one offspring (J9646) was assigned a father, but neither this nor other candidate males matched its sibling. The r-value for those potential half-siblings was 0.40, which was within the range of both half- and full siblings.

Discussion

Our study provided conclusive evidence for a polygamous mating system among wolverines (*cf.* Rausch & Pearson 1972). If reproduction in different years was taken into account, eight of 14 males that were assigned paternity in northern Sweden bred with more than one female. Moreover, eight of 13 females of which more than one litter was sampled (and where paternity was resolved in at least one) bred with more than one male. Partner shift was potentially a consequence of change of the resident male in the area. In general, when telemetry and genetic data was combined, breeding pairs were found to have overlapping territories.

In populations with polygamous mating, the effective population size may be reduced relative to

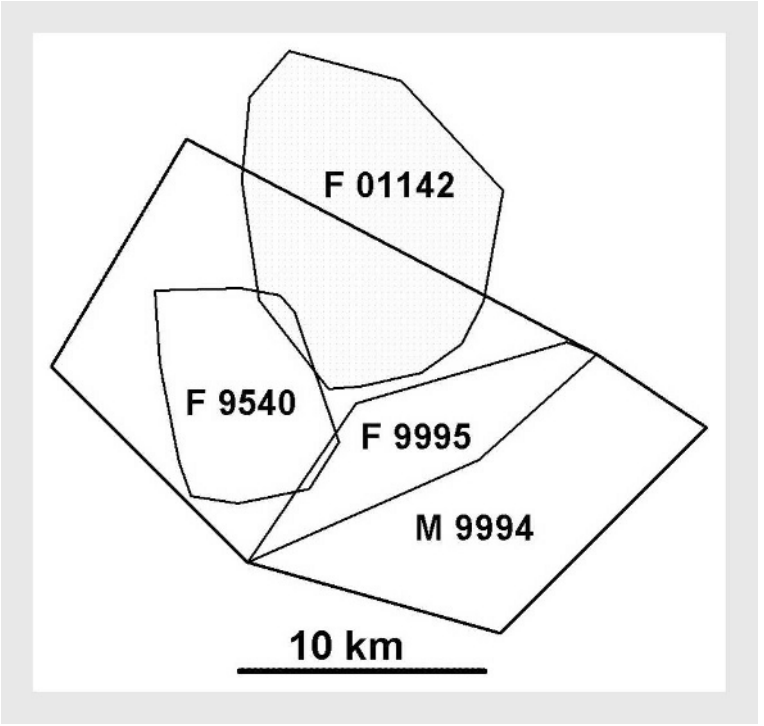

Figure 4. Spatial distribution (100% MCP home ranges) of three reproductive females and the male who were assigned paternity to their offspring, illustrating that the male home range fully or partly overlap those of the females. In 1999 the male reproduced both with F9540 and F9995 whereas in 2001 he reproduced with both F9995 and F01142.

a monogamous population with the same number of breeding pairs (Frankham et al. 2002). However, the difference between the number of breeding male and female wolverines appears to be relatively small. No male was found to breed with more than two females within a single year or with more than three females across all years. In northern Sweden during 1999-2004 (i.e. when a large proportion of all paternities were resolved) the observed male-to-female ratio of reproducing adults was 0.84. Note, however, that only offspring that survived until the age of 2-3 months were sampled. At this time, an average of 37% of females in the area had offspring, while an average of 53% was confirmed reproducing and most adult wolverine females are presumed to mate every year (Persson et al. 2006). Therefore, our analysis was likely to underestimate the number of females mated by a specific male each year.

Male wolverines defend territories that overlap those of a few females but territories are non-overlapping within sexes (Magoun 1985, Banci 1994). Given that the sex ratio in wolverine populations appears to be about 50:50 (Flagstad et al. 2004), this suggests that there is a fraction of males without defined territories. Thus, there may be stray males that mate with females within the territories of other males. If this is the case, one should expect to find litters fathered by a different male than the one holding the territory. However, no such observations were made as judged from cases where telemetry data were available. This could be explained by low mating success among stray males. Intraspecific predation (infanticide) is known to be an important cause of juvenile mortality among wolverines (Persson et al. 2003). Thus, another potential explanation might be that offspring fathered by stray males face increased intraspecific mortality from infanticide before they are sampled.

Multiple paternity is known to occur in several mustelids (Yamaguchi et al. 2004, Carpenter et al. 2005, Holland & Gleeson 2005). Multiple paternity is usually detected by counting paternal alleles in litters of three or more offspring (e.g. Say et al. 1999, Burton 2002, Morrison et al. 2002, Solomon et al. 2004). Likelihood based paternity tests may also be used, as assignments of different fathers to siblings in the same litter are indicative of multiple paternity (Burton 2002, Haynie et al 2003, Winters & Waser 2003, Burland et al. 2004). However, data from our study indicate that multiple paternity, if it occurs, is a rare phenomenon among Scandinavian wolverines. We detected only one potential litter, among a total of 32 (3%), in which multiple paternity may have occurred. This is lower than the incidence reported for other mustelids; in badgers *Meles meles* multiple paternity was observed in five of 31 examined litters (Carpenter et al. 2005), in mink *Mustela vison* in all of six litters (Yamaguchi et al. 2004) and in stoat *Mustela erminea* in one of five litters (Holland & Gleeson 2005). It can be hypothesised that the low frequency of multiple paternity in wolverines should be seen in relation to their solitary lifestyle, low population densities and strong male territoriality.

Relatively few loci can provide sufficient resolution for parentage tests at the level of genetic variation seen in outbred mammal populations (e.g. Say et al. 1999, Hughes et al. 2003). However, the ability to distinguish between orders of relatives (e.g. half- and full siblings) decreases rapidly with lower heterozygosity (Blouin et al. 1996, Blouin 2003). As a result of the low genetic variation in our study populations, the r-values showed a large overlap between different classes of relatives (see Fig. 2) and could not readily be used to separate first and second order relatives. For this to become possible, extended marker sets would be needed. Paternity assignment was assisted by our ability to define a refined list of candidate males as provided by telemetry data (e.g. age, year of death and other relationships). The lack of such data from the population in southern Norway likely explains why the ability to unambiguously infer paternity was lower in this population.

Acknowledgements - financial support was obtained from the Norwegian Directorate for Nature Management, the Swedish Environmental Protection Agency and WWF Sweden. Thanks to the Conservation Genetics group at the department of Evolutionary Biology, Uppsala University, for helpful discussion.

References

Banci, V. 1994: Wolverine. - In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Lyon, L.J. & Zielinski, W.J. (Eds.); The scientific basis for conserving forest carnivores. American marten, fisher, lynx and wolverine in the United States. U. S. Forest Service General Technical Report RM-254, Fort Collins, Colorado, USA, pp. 99-127.

Banci, V. & Harestad, A.S. 1988: Reproduction and natality of wolverines (Gulo gulo) in Yukon. - Annales Zoologici Fennici 25: 265-270.

Blouin, M.S. 2003: DNA-based methods for pedigree reconstruction and kinship analysis in natural populations. - Trends in Ecology and Evolution 18: 503-511.

Blouin, M.S., Parsons, M., Lacaille, V. & Lotz, S. 1996: Use of microsatellite loci to classify individuals by relatedness. - Molecular Ecology 5: 393-401.

Burland, T.M., Bennett, N.C., Jarvis, J.U. & Faulkes, C.G. 2004: Colony structure and parentage in wild colonies of co-operatively breeding Damaraland mole-rats suggest incest avoidance alone may not maintain reproductive skew. - Molecular Ecology 13: 2371-2379.

Burton, C. 2002: Microsatellite analysis of multiple paternity and male reproductive success in the promiscuous snowshoe hare. - Canadian Journal of Zoology 80: 1948-1956.

Carpenter, P.J., Pope, L.C., Greig, C., Dawson, D.A., Rogers, L.M., Erven, K., Wilson, G.J., Delahay, R.J., Cheeseman, C.L. & Burke, T. 2005: Mating system of the Eurasian badger, Meles meles, in a high density population. - Molecular Ecology 14: 273-284.

Constable, J.L., Ashley, M.V., Goodall, J. & Pusey, A.E. 2001: Noninvasive paternity assignment in Gombe chimpanzees. - Molecular Ecology 10: 1279-1300.

Dallas, J.F. & Piertney, S.B. 1998: Microsatellite primers for the Eurasian otter. - Molecular Ecology 7: 1248-1251.

Davis, C.S. & Strobeck, C. 1998: Isolation, variability and cross-species amplification of polymorphic microsatellite loci in the family Mustalidae. - Molecular Ecology 7: 1776-1778.

Duffy, A.J., Landa, A., O'Conell, M., Stratton, C. & Wright, J.M. 1998: Four polymorphic microsatellites in wolverine, Gulo gulo. - Animal Genetics 29: 63-72.

Flagstad, Ø., Brøseth, H., Hedmark, E., Wärdig, C., Johansson, M. & Ellegren, H. 2005: Populasjonsovervåking av jerv i Skandinavia ved hjelp av DNA-analyse fra ekskrementer. Rapport 41. - Norsk institutt for naturforskning. Trondheim, Norway, 46 pp. (In Norwegian).

Flagstad, Ø., Hedmark, E., Landa, A., Brøseth, H., Persson, J., Andersen, R., Segerström, P. & Ellegren, H. 2004: Colonization history and noninvasive monitoring of a reestablished wolverine population. - Conservation Biology 18: 676-688.

Frankham, R., Ballou, J.D. & Briscoe, D.A. 2002: Introduction to conservation genetics. Cambridge University Press, Cambridge, 640 pp.

Garnier, J.N., Bruford, M.W. & Goossens, B. 2001: Mating system and reproductive skew in black rhinoceros. - Molecular Ecology 10: 2031-2041.

Girman, D.J., Mills, M.G.L., Geffen, E. & Wayne, R.K. 1997: A molecular genetic analysis of social structure, dispersal and interpack relationships of the African wild dog (Lycaon pictus). - Behavioral Ecology and Sociobiology 40: 187-198.

Goodnight, K.F. & Queller, D.C. 1999: Computer software for performing likelihood tests of pedigree relationship using genetic markers. - Molecular Ecology 8: 1231-1234.

Haynie, M.L., van Den Bussche, R.A., Hoogland, J.L. & Gilbert, D.A. 2003: Parentage, multiple paternity, and breeding success in Gunnison's and Utah prairie dogs. - Journal of Mammalogy 84: 1244-1253.

Hedmark, E., Flagstad, Ø., Segerström, P., Persson, J., Landa, A. & Ellegren, H. 2004: DNA-based individual and sex identification from wolverine (Gulo gulo) faeces and urine. - Conservation Genetics 5: 405-410.

Holland, O.J. & Gleeson, D.M. 2005: Genetic characterisation of blastocysts and the identification of an instance of multiple parternity in the stoat (Mustela erminea). - Conservation Genetics 6: 855-858.

Huck, M., Lottker, P., Bohle, U.R. & Heymann, E.W. 2005: Paternity and kinship patterns in polyandrous moustached tamarins (Saguinus mystax). - American Journal of Physical Anthropology 4: 449-464.

Hughes, J.M., Mather, P.B., Toon, A., Ma, J., Rowley, I. & Russell, E. 2003: High levels of extra-group paternity in a population of Australian magpies Gumnorhina tibicen: evidence from microsatellite analysis. - Molecular Ecology 12: 3441-3450.

Kovach, A.I. & Powell, R.A. 2003: Effects of body size on male mating tactics and paternity in black bears, Ursus americanus. - Canadian Journal of Zoology 81: 1257-1268.

Kyle, C.J. & Strobeck, C. 2001: Genetic structure of North American wolverine (Gulo gulo) populations. - Molecular Ecology 10: 337-347.

Kyle, C.J. & Strobeck, C. 2002: Connectivity of peripheral and core populations of North American wolverines. - Journal of Mammalogy 83: 1141-1150.

Landa, A., Lindén, M. & Kojola, I. 2000: Action Plan for the Conservation of Wolverines (Gulo gulo) in Europe. - The Council of Europe, Concile of Europe Publishing, Nature and Environment T-115, 45 pp.

Landa, A., Tufto, J., Franzén, R., Bø, T., Lindén, M. & Swenson, J.E. 1998: Active wolverine Gulo gulo dens as a minimum population estimator in Scandinavia. - Wildlife Biology 4: 159-168.

Magoun, A.J. 1985: Population characteristics, ecology and management of wolverines in north-western Alaska. - PhD thesis, University of Alaska, Fairbanks, Alaska, 197 pp.

Marshall, T.C., Slate, J., Kruuk, L.E. & Pemberton, J.M. 1998: Statistical confidence for likelihood-based paternity inference in natural populations. - Molecular Ecology 7: 639-655.

Moritz, C., Heideman, A., Geffen, E. & McRae, P. 1997: Genetic population structure of the Greater Bilby Macrotis lagotis, a marsupial in decline. - Molecular Ecology 6: 925-936.

Morrison, S.F., Keogh, J.S. & Scott, I.A.W. 2002: Molecular determination of paternity in a natural popula-

tion of the multiply mating polygynous lizard Eulamprus heatwolei. - Molecular Ecology 11: 535-545.
O'Connell, M., Wright, J.M. & Farid, A. 1996: Development of PCR primers for nine polymorphic American mink Mustela vison microsatellite loci. - Molecular Ecology 5: 311-312.
Persson, J. 2003: Population ecology of Sandinavian wolverines. - PhD thesis, Swedish University of Agricultural Sciences, Umeå, Sweden, 40 pp.
Persson, J., Landa, A., Andersen, R. & Segerström, P. 2006: Reproductive characteristics of female wolverines (Gulo gulo) in Scandinavia. - Journal of Mammalogy 87: 75-79.
Persson, J., Willebrand, T., Landa, A., Andersen, R. & Segerström, P. 2003: The role of intraspecific predation in the survival of juvenile wolverines Gulo gulo. - Wildlife Biology 9: 21-28.
Queller, D.C. & Goodnight, K.F. 1989: Estimating relatedness using genetic markers. - Evolution 43: 258-275.
Rausch, R.A. & Pearson, A.M. 1972: Notes on the wolverine in Alaska and the Yukon territory. - Journal of Wildlife Management 36: 249-268.
Raymond, M. & Rousset, F. 1995: GENEPOP (version 1.2): a population genetics software for exact tests and ecumenicism. - Journal of Heredity 86: 248-249.
Rice, W.R. 1989: Analysing tables of statistical tests. - Evolution 43: 223-225.
Sambrook, E., Fritsch, F. & Maniatis, T. 1989: Molecular cloning, Cold Spring Harbor Laboratory Press, Cold Spring Harbor, New York, 2344 pp.
Say, L., Pontier, D. & Natoli, E. 1999: High variation in multiple paternity of domestic cats (Felis catus L.) in relation to environmental conditions. - Proceedings of the Royal Society of London B: Biological Sciences 266: 2071-2074.
Solomon, N.G., Keane, B., Knoch, L.R. & Hogan, P.J. 2004: Multiple paternity in socially monogamous prairie voles (Microtus ochrogaster). - Canadian Journal of Zoology 82: 1667-1671.
Valière, N. 2002: GIMLET: a computer program for analysing genetic individual identification data. - Molecular Ecology Notes 2: 377-379.
Walker, C., Vilá, C., Landa, A., Lindén, M. & Ellegren, H. 2001: Genetic variation and population structure in Scandinavian wolverine (Gulo gulo) populations. - Molecular Ecology 10: 53-63.
Winters, J.B. & Waser, P.M. 2003: Gene dispersal and outbreeding in a philopatric mammal. - Molecular Ecology 12: 2251-2259.
Yamaguchi, N., Sarno, R.J., Johnson, W.E., O'Brien, S.J. & MacDonald, D.W. 2004: Multiple paternity and reproductive tactics of free-ranging American minks, Mustela vison. - Journal of Mammalogy 85: 432-439.

Appendix I

Offspring for which paternity was resolved, sorted after their mothers. LOD-score for the assigned father and relatedness (r) values for mother-offspring (M-O), father-offspring (F-O) and mother-father (M-F) are provided. The study area in northern Sweden was divided into central part (core) and periphery (perip).

Offspring	Mother	Birth year	Group	Father	LOD-score	r M-O	r F-O	r M-F
J9420	J9424	1994	core 93-98	J8907	8.79	0.42	0.52	-0.08
J99103	J9540	1999	core 99-04	J9994	7.35	0.29	0.37	-0.26
J99104	J9540	1999	core 99-04	J9994	7.97	0.21	0.45	-0.26
J01144	J9540	2001	core 99-04	J9994	5.42	0.38	0.34	-0.26
J01127	J9541	2001	core 99-04	J9991	7.84	0.58	0.53	0.16
J01128	J9541	2001	core 99-04	J9991	6.84	0.60	0.46	0.16
J01129	J9541	2001	core 99-04	J9991	10.29	0.55	0.60	0.16
J02158	J9541	2002	core 99-04	J9991	7.61	0.50	0.60	0.16
J02159	J9541	2002	core 99-04	J9991	7.50	0.60	0.44	0.16
J9646	J9643	1996	core 93-98	J9418	7.16	0.40	0.39	-0.29
J9656	J9647	1996	core 93-98	J9652	6.00	0.48	0.62	0.13
J00110	J9650	2000	core 99-04	J01122	8.26	0.62	0.72	0.23
J00111	J9650	2000	core 99-04	J01122	6.16	0.67	0.61	0.23
J01126	J9650	2001	core 99-04	J01122	4.56	0.62	0.56	0.23
J01132	J9650	2001	core 99-04	J01122	4.44	0.57	0.62	0.23
J9653	J9651	1996	core 93-98	J99100	8.60	0.24	0.33	-0.60
J9654	J9651	1996	core 93-98	J99100	5.81	0.31	0.35	-0.60
J9997	J9759	1999	perip 99-04	J9984	5.96	0.40	0.37	-0.14
J9875	J9869	1998	core 93-98	J9423	8.97	0.21	0.68	-0.04
J02162	J9869	2002	core 99-04	J00120	8.11	0.33	0.51	-0.21
J03176	J9869	2003	core 99-04	J00120	7.59	0.24	0.51	-0.21
J04187	J9869	2004	core 99-04	J00120	5.45	0.30	0.45	-0.21

Appendix I. Continued

Offspring	Mother	Birth year	Group	Father	LOD-score	r M-O	r F-O	r M-F
J00113	J9870	2000	core 99-04	J9766	7.06	0.42	0.59	-0.14
J00114	J9870	2000	core 99-04	J9766	7.01	0.32	0.39	-0.14
J00115	J9870	2000	core 99-04	J9766	5.41	0.47	0.33	-0.14
J02152	J9870	2002	core 99-04	J9766	5.40	0.39	0.49	-0.16
J9878	J9873	1998	core 93-98	J9423	6.54	0.32	0.57	-0.14
J99101	J9873	1999	core 99-04	J9423	4.40	0.35	0.49	-0.14
J99102	J9873	1999	core 99-04	J9423	5.51	0.45	0.53	-0.14
J00118	J9873	2000	core 99-04	J99100	4.44	0.61	0.54	0.29
J00119	J9873	2000	core 99-04	J99100	8.88	0.53	0.66	0.29
J9998	J9985	1999	perip 99-04	J9984	6.54	0.49	0.33	-0.15
J9999	J9985	1999	perip 99-04	J9984	8.37	0.53	0.37	-0.15
J04189	J9986	2004	core 99-04	J04180	8.59	0.37	0.45	-0.02
J01146	J9987	2001	perip 99-04	J99105	5.22	0.45	0.53	0.04
J01147	J9987	2001	perip 99-04	J99105	10.18	0.31	0.75	0.11
J02156	J9987	2002	perip 99-04	J99105	8.11	0.49	0.50	0.11
J02157	J9987	2002	perip 99-04	J99105	6.30	0.56	0.51	0.11
J99106	J9993	1999	core 99-04	J99105	8.17	0.65	0.68	0.22
J99107	J9993	1999	core 99-04	J99105	6.07	0.73	0.49	0.22
J9986	J9995	1999	core 99-04	J9994	6.68	0.26	0.50	-0.11
J01137	J01124	2001	perip 99-04	J03178	12.64	0.30	0.39	-0.46
J02163	J01124	2002	perip 99-04	J03178	13.55	0.19	0.34	-0.46
J01133	J01125	2001	core 99-04	J99105	8.49	0.30	0.60	0.00
J02155	J01125	2002	core 99-04	J99105	7.78	0.31	0.68	0.00
J02166	J01125	2002	core 99-04	J99105	4.60	0.34	0.68	-0.02
J04184	J01129	2004	core 99-04	J9766	6.25	0.53	0.53	0.12
J04190	J01129	2004	core 99-04	J9766	8.16	0.52	0.60	0.12
J01135	J01142	2001	core 99-04	J9994	9.14	0.42	0.56	-0.18
J01143	J01142	2001	core 99-04	J9994	8.98	0.41	0.52	-0.18
J02153	J01142	2002	core 99-04	J9994	8.64	0.30	0.57	-0.18
J02154	J01142	2002	core 99-04	J9994	8.07	0.51	0.51	-0.18
J03173	J01142	2003	core 99-04	J9994	8.10	0.46	0.44	-0.18
J03174	J01142	2003	core 99-04	J9994	9.01	0.19	0.70	-0.18
J03168	J03167	2003	perip 99-04	J01122	5.46	0.51	0.66	0.18
J03169	J03167	2003	perip 99-04	J01122	4.48	0.54	0.56	0.18
J03175	J03171	2003	core 99-04	J9991	6.37	0.46	0.32	-0.16
V012	Ind12	2001	S Norway	Ind4	9.81	0.32	0.58	-0.39
V013	Ind12	2001	S Norway	Ind4	3.79	0.34	0.43	-0.39
R009	Ind33	2003	S Norway	Ind47	5.77	0.24	0.51	-0.03
R010	Ind33	2003	S Norway	Ind47	6.47	0.53	0.47	-0.03
R016	Ind33	2004	S Norway	Ind47	5.49	0.29	0.44	-0.03
R017	Ind33	2004	S Norway	Ind47	7.55	0.20	0.50	-0.03
R003	Ind46	2003	S Norway	Ind136	11.77	0.46	0.52	-0.10
R014	Ind46	2003	S Norway	Ind136	15.66	0.38	0.55	-0.10
R015	Ind46	2003	S Norway	Ind136	8.27	0.40	0.50	-0.10
R001	Ind57	2004	S Norway	Ind85	4.03	0.64	0.38	0.10
R002	Ind57	2004	S Norway	Ind85	5.67	0.36	0.69	0.10
V028	Ind89	2004	S Norway	Ind41	6.21	0.39	0.36	-0.40
V029	Ind89	2004	S Norway	Ind41	4.38	0.23	0.39	-0.35
V026	Ind121	2004	S Norway	Ind140	4.92	0.26	0.46	-0.02
V027	Ind121	2004	S Norway	Ind140	7.40	0.42	0.48	-0.02
V030	Ind146	2004	S Norway	Ind715	4.41	0.56	0.29	-0.08
V031	Ind146	2004	S Norway	Ind715	5.56	0.61	0.29	-0.08

Appendix II

Outcome of the paternity tests for each litter. When a father could not be assigned, the male is marked as unknown (unkn.). The potential case of multiple paternity is indicated in italics.

	Year											
Female	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
Northern Sweden												
J9312	unkn.											
J9315	unkn.											
J9419			unkn.		unkn.							
J9424		J8907										
J9525					unkn.							
J9527			unkn.									
J9530			unkn.									
J9533			unkn.									
J9538			unkn.									
J9540			unkn.	unkn.		unkn.	J9994		J9994			
J9541									J9991	J9991		
J9643				*J9418/ unkn.*								
J9646										unkn.		
J9647				J9652		unkn.						
J9648				unkn.								
J9650				unkn.				J01122	J01122			
J9651				J99100		unkn.						
J9759							J9984					
J9869						J9423				J00120	J00120	J00120
J9870						unkn.		J9766	J9766*	J9766		
J9873						J9423	J9423	J99100				
J9879									unkn.			unkn.
J9985							J9984					
J9986												J04180
J9987							unkn.		J99105	J99105		
J9993							J99105					
J9995							J9994					
J99101										unkn.		
J00112								unkn.				
J01124									J03178	J03178		
J01125									J99105	J99105		
J01129												J9766
J01130									J9766			
J01142									J9994	J9994	J9994	
J01148									unkn.	unkn.		
J03167											J01122	
J03171											J9991	
Southern Norway												
Ind12									Ind4			
Ind21									unkn.			
Ind23											unkn.	
Ind32											unkn.	
Ind33											Ind47	Ind47
Ind46											Ind136	
Ind50									unkn.			
Ind51									unkn.			
Ind57												Ind85
Ind89												Ind41
Ind97												unkn.
Ind104											unkn.	
Ind121												Ind140
Ind145												unkn.
Ind146												Ind715

* Presumably J9766 was the father although he could not be assigned according to the criteria; further information is provided in Appendix III.

Appendix III

Supplementary material

A few dubious cases of paternity (mainly inconsistent observations from genetics and telemetry) were encountered and data from these cases were not included in further analyses. A detailed account for all these cases is given below.

The offspring J01140 had two candidate males showing significant LOD scores as potential father (J00120, LOD = 4.82; J9766, LOD = 3.90). However, we did not assign the male with the highest LOD-score as father since J00120, equipped with a radio transmitter, was never observed closer than 28 km to the outermost range of the territory of J9870, the mother of J01140. In contrast, J9766 had overlapping territory with J9870. J9766 was unambiguously assigned paternity to all other offspring of J9870 (both older and younger than J01140). In addition, relatedness analysis revealed that J00120 and J9766 were closely related (r = 0.56), J00120 could therefore potentially be a brother or an uncle to J01140, which would explain why he appeared as a likely candidate.

In a similar case, J03131 was not assigned a father because the second best candidate, J9766 (LOD = 5.01), appeared more likely than the first candidate, J9880 (LOD = 5.59). J9766 and J03131's mother (J01130) were known to have overlapping territories, while J9880 remained in the area where he was born, 30-40 km away from J01130's territory, until March in the year of mating. Radio-contact with J9880 was lost in March, probably as a result of dispersal. It seems unlikely that he dispersed 30-40 km and then immediately, as young (two years old) and inexperienced, was able to mate within the territory of an older well-established male. Moreover, J9880 was closely related to J9766 (r = 0.61).

For a third offspring (J03170), the male J01123 was not assigned paternity although he fulfilled all criteria. However, from telemetry data he was known to be dispersing from his previous area and to be > 100 km from the territory of J03170's mother (J03171) when radio-contact with him was broken just before the actual breeding season. Moreover, J01123 was closely related to J9991 (r = 0.61) who was assigned as the father to J03170's sibling in the same litter. J9991 came out as the second most likely candidate for J03170 although there was one mismatching loci and a low LOD-score (1.46). The r-value between J03170 and J9991 was also low (0.19). However, when re-running the paternity test and relatedness analysis without providing a genotype for J03170 at the mismatching loci, it appeared as if that particular mismatch had a strong effect both on LOD-score and r-value as the results obtained now were within the requirements for assignment (LOD = 4.04 and r = 0.31). In this case, we did not assign J9991 as the father to J03170, but neither did we consider it to be a likely case of multiple paternity.

For offspring J9655, J02164, J01145 and JJ03172, paternity could not be assigned although the male with the highest LOD-score appeared likely (as judging from father assignments of their siblings and overlapping male and female territories), due to the r-value between the respective offspring and the male being slightly below the required cut-off value. In each of these cases the male fulfilled the criteria for the particular offspring's siblings and was assigned for those.

Finally, if the pattern of paternity allocation for siblings within litters was dubious in a such way that it appeared as if the siblings were fathered by a male with a similar genotype (e.g. if the most likely male for one sibling appeared as the second or third most likely for the other siblings and vice versa), paternity was not assigned to any of the siblings even if one or more could have been assigned a father according to the criteria. This was done because such a pattern may indicate that the siblings in the litter were fathered by the same male, but that he was not sampled. In southern Norway, paternity of six offspring (R019, Ind170, R011, V009, V010 and V015) in four different litters was not assigned although at least one male fulfilled the assignment criteria because the pattern of paternity allocation within the litters indicated that the offspring could be full-siblings fathered by a non-sampled male.

Appendix Table 1. Details on all offspring included in paternity tests. The information is sorted in the order of group, mother and offspring birth year. All candidate males with LOD ≥ 3.0 are shown. If there is more than one candidate for an offspring, those are given on separate rows. In cases where a male was assigned as the father although he showed a mismatch at one locus, relatedness values for the parent-offspring trio was recalculated without providing a genotype for the putative father at the mismatching loci. Abbreviations: r = relatedness value; M = mother, O = offspring, CP = candidate parent, peri = periphery.

Offspring	Mother	Birth year	Group	Candidate father	LOD-score	r M-O	r CP-O	r M-CP	Alleles mismatching (loci compared for M-O-CP)	Decision/comment for candidate fathers
J9311	J9312	1993	perip 93-98	-	-	0.33	-	-	-	-
J9313	J9312	1993	perip 93-98	-	-	0.34	-	-	-	-
J9542	J9527	1995	perip 93-98	-	-	0.21	-	-	-	-
J9528	J9530	1995	perip 93-98	-	-	0.51	-	-	-	-
J9529	J9530	1995	perip 93-98	-	-	0.35	-	-	-	-
J9316	J9315	1993	core 93-98	J9314	6.14	0.52	0.62	0.39	0 (20)	M-CP too high
J9317	J9315	1993	core 93-98	J9314	5.60	0.47	0.59	0.39	0 (20)	M-CP too high
J9534	J9419	1995	core 93-98	-	-	0.44	-	-	-	-
J9535	J9419	1995	core 93-98	-	-	0.42	-	-	-	-
J9763	J9419	1997	core 93-98	-	-	0.49	-	-	-	-
J9764	J9419	1997	core 93-98	-	-	0.54	-	-	-	-
J9420	J9424	1994	core 93-98	J8907	8.79	0.42	0.52	-0.08	0 (20)	Assigned
J9762	J9525	1997	core 93-98	-	-	0.41	-	-	-	-
J9526	J9533	1995	core 93-98	-	-	0.36	-	-	-	-
J9531	J9533	1995	core 93-98	-	-	0.36	-	-	-	-
J9532	J9533	1995	core 93-98	-	-	0.35	-	-	-	-
J9539	J9538	1995	core 93-98	-	-	0.58	-	-	-	-
J9541	J9538	1995	core 93-98	-	-	0.63	-	-	-	-
J9995	J9540	1995	core 93-98	-	-	0.47	-	-	-	-
J9537	J9540	1995	core 93-98	-	-	0.27	-	-	-	-
J9649	J9540	1996	core 93-98	-	-	0.26	-	-	-	-
J9881	J9540	1998	core 93-98	-	-	0.25	-	-	-	-
J9882	J9540	1998	core 93-98	-	-	0.25	-	-	-	-
J9645	J9643	1996	core 93-98	-	-	0.46	-	-	-	-
J9646	J9643	1996	core 93-98	J9418	7.16	0.40	0.39	-0.29	0 (20)	Assigned
J9656	J9647	1996	core 93-98	J9652	6.00	0.48	0.62	0.13	0 (20)	Assigned
J9876	J9647	1998	core 93-98	-	-	0.64	-	-	-	-
J9877	J9647	1998	core 93-98	-	-	0.61	-	-	-	-
J9644	J9648	1996	core 93-98	J9984	5.20	0.25	0.12	-0.64	2 (20)	CP-O too low, 2 Mismatches
J9657	J9650	1996	core 93-98	-	-	0.63	-	-	-	-
J9658	J9650	1996	core 93-98	-	-	0.52	-	-	-	-
J9653	J9651	1996	core 93-98	J99100	8.60	0.24	0.33	-0.60	0 (20)	Assigned
J9654	J9651	1996	core 93-98	J99100	5.81	0.31	0.35	-0.60	0 (20)	Assigned
J9655	J9651	1996	core 93-98	J99100	9.45	0.10	0.26	-0.60	0 (20)	CP-O too low, dubious case discussed in Appendix III
				J9760	4.14	0.10	0.36	-0.14	2 (20)	2 mismatches
J9879	J9651	1998	core 93-98	J9766	4.96	0.74	0.68	0.59	0 (20)	M-CP too high
J9880	J9651	1998	core 93-98	J9423	3.82	0.43	0.70	0.41	3 (20)	M-CP too high, 3 mismatches
J9875	J9869	1998	core 93-98	J9423	8.97	0.21	0.68	-0.04	0 (20)	Assigned
J9871	J9870	1998	core 93-98	J9532	6.65	0.55	0.65	0.32	0 (20)	M-CP too high
				J9526	5.30	0.55	0.57	0.33	0 (20)	M-CP too high
J9872	J9870	1998	core 93-98	J9526	7.89	0.60	0.62	0.33	0 (20)	M-CP too high
J9874	J9870	1998	core 93-98	J9526	6.98	0.21	0.45	0.33	1 (20)	M-CP too high
				J9532	5.97	0.21	0.53	0.32	1 (20)	M-CP too high
J9878	J9873	1998	core 93-98	J9423	6.54	0.32	0.57	-0.14	1 (20)	Assigned
J01137	J01124	2001	perip 99-04	J03178	12.64	0.30	0.39	-0.46	0 (20)	Assigned
J02163	J01124	2002	perip 99-04	J03178	13.55	0.19	0.34	-0.46	0 (20)	Assigned
J02164	J01124	2002	perip 99-04	J03178	9.06	0.35	0.24	-0.46	0 (20)	CP-O too low, dubious case discussed in Appendix III
J03168	J03167	2003	perip 99-04	J00111	5.57	0.51	0.69	0.35	0 (20)	M-CP too high

Appendix III. Continued

Offspring	Mother	Birth year	Group	Candidate father	LOD-score	r M-O	r CP-O	r M-CP	Alleles mismatching (loci compared for M-O-CP)	Decision/comment for candidate fathers
				J01122	5.46	0.51	0.66	0.18	0 (20)	Assigned
				J9766	4.79	0.51	0.70	0.33	0 (20)	M-CP too high
J03169	J03167	2003	perip 99-04	J01122	4.48	0.54	0.56	0.18	0 (19)	Assigned
J01131	J01130	2001	perip 99-04	J9880	5.59	0.45	0.57	0.00	0 (20)	Dubious case, discussed in Appendix III
				J9766	5.01	0.45	0.58	0.17	0 (20)	Not assigned according to above
J9997	J9759	1999	perip 99-04	J9984	5.96	0.40	0.37	-0.14	0 (20)	Assigned
J9998	J9985	1999	perip 99-04	J9984	6.54	0.49	0.33	-0.15	0 (20)	Assigned
J9999	J9985	1999	perip 99-04	J9984	8.37	0.53	0.37	-0.15	0 (20)	Assigned
J9988	J9987	1999	perip 99-04	-	-	0.41	-	-	-	-
J9989	J9987	1999	perip 99-04	-	-	0.45	-	-	-	-
J01146	J9987	2001	perip 99-04	J99105	5.22	0.45	0.53	0.04	1 (20)	Assigned
J01147	J9987	2001	perip 99-04	J99105	10.18	0.31	0.75	0.11	0 (20)	Assigned
J02156	J9987	2002	perip 99-04	J99105	8.11	0.49	0.50	0.11	0 (20)	Assigned
				J9766	4.32	0.49	0.40	0.07	1 (20)	Other male assigned
J02157	J9987	2002	perip 99-04	J99105	6.30	0.56	0.51	0.11	0 (20)	Assigned
J00116	J00112	2000	core 99-04	J99100	8.40	0.64	0.78	0.47	0 (20)	M-CP too high
				J9994	5.51	0.64	0.79	0.57	1 (20)	M-CP too high
J00117	J00112	2000	core 99-04	J99100	5.80	0.63	0.77	0.47	0 (20)	M-CP too high
				J9994	5.47	0.63	0.79	0.57	1 (20)	M-CP too high
J01133	J01125	2001	core 99-04	J99105	8.49	0.30	0.60	0.00	0 (20)	Assigned
				J9880	4.79	0.30	0.54	0.06	1 (20)	Other male assigned
				J9766	4.35	0.30	0.49	-0.06	1 (20)	Other male assigned
J02155	J01125	2002	core 99-04	J99105	7.78	0.31	0.68	0.00	0 (20)	Assigned
				J9766	5.91	0.31	0.42	-0.06	0 (20)	Other male assigned
J02166	J01125	2002	core 99-04	J99105	4.60	0.34	0.68	-0.02	1 (20)	Assigned
J04184	J01129	2004	core 99-04	J9766	6.25	0.53	0.53	0.12	0 (19)	Assigned
				J01122	4.87	0.53	0.35	-0.22	0 (19)	Other male assigned
				J9653	3.68	0.53	0.45	0.22	1 (20)	Other male assigned
J04190	J01129	2004	core 99-04	J9766	8.16	0.52	0.60	0.12	0 (19)	Assigned
				J01122	4.45	0.52	0.41	-0.22	1 (19)	Other male assigned
J01135	J01142	2001	core 99-04	J9994	9.14	0.42	0.56	-0.18	0 (20)	Assigned
				J99100	3.76	0.42	0.37	-0.35	1 (20)	Other male assigned
J01143	J01142	2001	core 99-04	J9994	8.98	0.41	0.52	-0.18	0 (20)	Assigned
				J99100	7.04	0.41	0.41	-0.35	0 (20)	Other male assigned
J02153	J01142	2002	core 99-04	J9994	8.64	0.30	0.57	-0.18	0 (20)	Assigned
J02154	J01142	2002	core 99-04	J9994	8.07	0.51	0.51	-0.18	0 (20)	Assigned
J03173	J01142	2003	core 99-04	J9994	8.10	0.46	0.44	-0.18	0 (19)	Assigned
J03174	J01142	2003	core 99-04	J9994	9.01	0.19	0.70	-0.18	0 (19)	Assigned
				J99100	7.70	0.19	0.57	-0.35	0 (19)	Other male assigned
J01136	J01148	2001	core 99-04	-	-	0.41	-	-	-	-
J01149	J01148	2001	core 99-04	-	-	0.51	-	-	-	-
J02160	J01148	2002	core 99-04	-	-	0.54	-	-	-	-
J02161	J01148	2002	core 99-04	J9989	7.45	0.54	0.78	0.43	0 (20)	M-CP too high
J03170	J03171	2003	core 99-04	J01123	3.39	0.55	0.27	-0.32	1 (20)	Dubious case, discussed in Appendix III
J03175	J03171	2003	core 99-04	J9991	6.37	0.46	0.32	-0.16	0 (19)	Assigned
				J04180	4.10	0.46	0.26	-0.30	2 (20)	2 mismatches
J99103	J9540	1999	core 99-04	J9994	7.35	0.29	0.37	-0.26	0 (20)	Assigned
J99104	J9540	1999	core 99-04	J9994	7.97	0.21	0.45	-0.26	0 (20)	Assigned
				J99100	5.35	0.21	0.19	-0.36	0 (20)	CP-O too low
J01144	J9540	2001	core 99-04	J9994	5.42	0.38	0.34	-0.26	0 (20)	Assigned
				J01123	3.57	0.38	0.29	-0.26	0 (20)	Other male assigned
				J99100	3.14	0.38	0.32	-0.36	1 (20)	Other male assigned
J01145	J9540	2001	core 99-04	J9994	6.24	0.38	0.25	-0.26	0 (20)	CP-O too low, dubious case, discussed in Appendix III

Appendix III. Continued

Offspring	Mother	Birth year	Group	Candidate father	LOD-score	r M-O	r CP-O	r M-CP	Alleles mismatching (loci compared for M-O-CP)	Decision/comment for candidate fathers
J01127	J9541	2001	core 99-04	J9991	7.84	0.58	0.53	0.16	0 (20)	Assigned
				J01123	4.77	0.58	0.75	0.64	2 (20)	M-CP too high, 2 mismatches
J01128	J9541	2001	core 99-04	J9991	6.84	0.60	0.46	0.16	0 (20)	Assigned
J01129	J9541	2001	core 99-04	J9991	10.29	0.55	0.60	0.16	0 (20)	Assigned
J02158	J9541	2002	core 99-04	J9991	7.61	0.50	0.60	0.16	0 (20)	Assigned
J02159	J9541	2002	core 99-04	J9991	7.50	0.60	0.44	0.16	0 (20)	Assigned
J02150	J9646	2002	core 99-04	-	-	0.56	-	-	-	-
J02151	J9646	2002	core 99-04	-	-	0.49	-	-	-	-
J00110	J9650	2000	core 99-04	J01122	8.26	0.62	0.72	0.23	0 (20)	Assigned
J00111	J9650	2000	core 99-04	J01122	6.16	0.67	0.61	0.23	0 (20)	Assigned
				J9766	4.98	0.67	0.61	0.38	0 (20)	Other male assigned
J01126	J9650	2001	core 99-04	J01122	4.56	0.62	0.56	0.23	1 (20)	Assigned
				J9992	4.47	0.62	0.38	0.09	1 (20)	Other male assigned
J01132	J9650	2001	core 99-04	J01122	4.44	0.57	0.62	0.23	1 (20)	Assigned
J02162	J9869	2002	core 99-04	J00120	8.11	0.33	0.51	-0.21	0 (20)	Assigned
J03172	J9869	2003	core 99-04	J00120	4.78	0.54	0.26	-0.21	0 (19)	CP-O too low, dubious case, discussed in Appendix III
				J9989	3.78	0.54	0.36	0.14	0 (19)	Not assigned according to above
J03176	J9869	2003	core 99-04	J00120	7.59	0.24	0.51	-0.21	0 (20)	Assigned
				J9766	4.29	0.24	0.47	-0.27	1 (20)	Other male assigned
J04187	J9869	2004	core 99-04	J00120	5.45	0.30	0.45	-0.21	0 (20)	Assigned
				J00111	3.30	0.30	0.36	-0.16	0 (20)	Other male assigned
J00113	J9870	2000	core 99-04	J9766	7.06	0.42	0.59	-0.14	0 (20)	Assigned
J00114	J9870	2000	core 99-04	J9766	7.01	0.32	0.39	-0.14	0 (20)	Assigned
				J01123	3.95	0.32	0.31	-0.31	0 (20)	Other male assigned
J00115	J9870	2000	core 99-04	J9766	5.41	0.47	0.33	-0.14	0 (20)	Assigned
				J01122	3.09	0.47	0.33	-0.08	1 (20)	Other male assigned
J01140	J9870	2001	core 99-04	J00120	4.82	0.36	0.48	-0.14	0 (20)	Dubious case, discussed in Appendix III
				J9766	3.90	0.36	0.37	-0.14	0 (20)	Not assigned according to above
J02152	J9870	2002	core 99-04	J9766	5.40	0.39	0.45	-0.08	1 (20)	Assigned
				J9880	5.16	0.39	0.37	-0.03	1 (20)	Other male assigned
J99101	J9873	1999	core 99-04	J9423	4.40	0.35	0.49	-0.14	1 (20)	Assigned
J99102	J9873	1999	core 99-04	J9423	5.51	0.45	0.53	-0.14	1 (20)	Assigned
J00118	J9873	2000	core 99-04	J99100	4.44	0.61	0.54	0.29	0 (20)	Assigned
				J01123	3.59	0.61	0.21	0.05	2 (20)	CP-O too low, 2 mismatches
J00119	J9873	2000	core 99-04	J99100	8.88	0.53	0.66	0.29	0 (20)	Assigned
J01138	J9879	2001	core 99-04	-	-	0.64	-	-	-	-
J01139	J9879	2001	core 99-04	-	-	0.45	-	-	-	-
J04186	J9879	2004	core 99-04	J00120	6.94	0.63	0.64	0.32	0 (19)	M-CP too high
J02165	J99101	2002	core 99-04	J00120	3.29	0.36	0.68	0.32	2 (20)	M-CP too high, 2 mismatches
J04189	J9986	2004	core 99-04	J04180	8.59	0.37	0.45	-0.02	0 (19)	Assigned
J99106	J9993	1999	core 99-04	J99105	8.17	0.65	0.68	0.22	0 (20)	Assigned
				J9766	5.54	0.65	0.41	0.05	1 (20)	Other male assigned
J99107	J9993	1999	core 99-04	J99105	6.07	0.73	0.49	0.22	0 (20)	Assigned
J9986	J9995	1999	core 99-04	J9994	6.68	0.26	0.50	-0.11	0 (20)	Assigned
				J99100	4.69	0.26	0.33	-0.07	0 (20)	Other male assigned
R006	Ind104	2003	S Norway	Ind102	6.13	0.64	0.73	0.51	0 (16)	M-CP too high
				IndC	3.17	0.64	0.60	0.69	2 (17)	M-CP too high, 2 mismatches
R007	Ind104	2003	S Norway	IndC	7.49	0.70	0.76	0.69	0 (17)	M-CP too high
				Ind82	6.85	0.70	0.65	0.60	0 (17)	M-CP too high

Appendix III. Continued

Offspring	Mother	Birth year	Group	Candidate father	LOD-score	r M-O	r CP-O	r M-CP	Alleles mismatching (loci compared for M-O-CP)	Decision/comment for candidate fathers
				Ind102	6.49	0.70	0.76	0.51	0 (16)	M-CP too high
				Ind163	5.07	0.70	0.61	0.39	0 (16)	M-CP too high
R008	Ind104	2003	S Norway	Ind102	6.08	0.74	0.48	0.51	0 (16)	M-CP too high
				Ind14	5.05	0.74	0.48	0.34	0 (15)	M-CP too high
				Ind163	4.69	0.74	0.43	0.39	0 (16)	M-CP too high
				IndC	3.94	0.74	0.64	0.69	1 (17)	M-CP too high
V012	Ind12	2001	S Norway	Ind4	9.81	0.32	0.58	-0.39	0 (16)	Assigned
				Ind18	5.78	0.32	0.57	0.09	1 (16)	Other male assigned
				Ind98	5.68	0.32	0.63	0.06	1 (17)	Other male assigned
				Ind71	5.03	0.32	0.43	-0.04	1 (16)	Other male assigned
V013	Ind12	2001	S Norway	Ind4	3.79	0.34	0.43	-0.39	0 (14)	Assigned
				IndV020	3.44	0.34	0.51	-0.10	0 (13)	Other male assigned
V026	Ind121	2004	S Norway	Ind140	4.92	0.26	0.46	-0.02	0 (15)	Assigned
V027	Ind121	2004	S Norway	Ind140	7.40	0.42	0.48	-0.02	0 (19)	Assigned
				Ind10	4.54	0.42	0.48	0.08	1 (17)	Other male assigned
				Ind151	3.89	0.42	0.36	0.02	1 (19)	Other male assigned
				Ind1	3.02	0.42	0.19	-0.21	2 (19)	CP-O too low, 2 mismatches
R018	Ind145	2004	S Norway	Ind28	8.30	0.31	0.40	0.35	0 (19)	M-CP too high
R019	Ind145	2004	S Norway	Ind28	3.65	0.49	0.34	0.35	0 (19)	M-CP too high
				Ind10	3.06	0.49	0.40	0.03	1 (17)	dubious allocation, not assigned
V030	Ind146	2004	S Norway	Ind715	4.41	0.56	0.29	-0.08	0 (18)	Assigned
				Ind14	4.08	0.56	0.36	-0.15	0 (15)	Other male assigned
V031	Ind146	2004	S Norway	Ind715	5.56	0.61	0.29	-0.08	0 (18)	Assigned
V017	Ind21	2001	S Norway	Ind63	4.29	0.42	0.22	-0.37	0 (18)	CP-O too low
R004	Ind23	2003	S Norway	Ind31	7.01	0.24	0.23	-0.60	0 (17)	CP-O too low
				Ind27	4.90	0.24	0.05	-0.64	1 (17)	CP-O too low
				Ind129	4.67	0.24	0.27	-0.41	2 (16)	2 mismatches
				Ind85	4.42	0.24	0.13	-0.56	1 (19)	CP-O too low
				IndV006	4.32	0.24	-0.05	-0.56	1 (18)	CP-O too low
				Ind160	4.06	0.24	0.20	-0.29	1 (18)	CP-O too low
R005	Ind23	2003	S Norway	Ind31	3.61	0.24	0.09	-0.60	1 (17)	CP-O too low
Ind170	Ind32	2003	S Norway	Ind49	3.74	0.79	0.43	0.15	0 (16)	Dubious case, discussed in Appendix III
				Ind90	3.71	0.79	0.40	0.17	0 (19)	Not assigned according to above
				Ind91	3.59	0.79	0.52	0.30	1 (18)	M-CP too high
				Ind52	3.47	0.79	0.32	-0.09	1 (17)	Not assigned according to above
R011	Ind32	2003	S Norway	Ind90	5.76	0.61	0.61	0.16	0 (19)	Dubious case, discussed in Appendix III
				Ind119	4.68	0.61	0.51	0.03	1 (18)	Not assigned according to above
				Ind49	4.56	0.61	0.51	0.15	0 (16)	Not assigned according to above
				Ind143	3.71	0.61	0.33	0.21	1 (18)	Not assigned according to above
R009	Ind33	2003	S Norway	Ind47	5.77	0.24	0.51	-0.03	0 (17)	Assigned
R010	Ind33	2003	S Norway	Ind47	6.47	0.53	0.47	-0.03	0 (17)	Assigned
R016	Ind33	2004	S Norway	Ind47	5.49	0.29	0.44	-0.03	0 (18)	Assigned
				Ind28	3.17	0.29	0.47	-0.02	1 (19)	Other male assigned
R017	Ind33	2004	S Norway	Ind47	7.55	0.20	0.50	-0.03	0 (18)	Assigned
R003	Ind46	2003	S Norway	Ind136	11.77	0.46	0.52	-0.10	0 (18)	Assigned
R014	Ind46	2003	S Norway	Ind136	15.66	0.38	0.55	-0.10	0 (20)	Assigned
R015	Ind46	2003	S Norway	Ind136	8.27	0.40	0.50	-0.10	0 (20)	Assigned
				Ind142	5.52	0.40	0.26	-0.34	0 (19)	Other male assigned
				Ind28	4.16	0.40	0.20	-0.32	0 (19)	CP-O too low

Appendix III. Continued

Offspring	Mother	Birth year	Group	Candidate father	LOD-score	r M-O	r CP-O	r M-CP	Alleles mismatching (loci compared for M-O-CP)	Decision/comment for candidate fathers
				Ind141	3.86	0.40	0.33	-0.37	1 (19)	Other male assigned
V009	Ind50	2001	S Norway	Ind119	5.53	0.37	0.46	-0.01	1 (18)	Dubious case, discussed in Appendix III
				IndV003	5.05	0.37	0.42	-0.20	1 (18)	Not assigned according to above
				Ind90	3.13	0.37	0.36	-0.08	2 (18)	2 mismatches
V010	Ind50	2001	S Norway	IndV003	7.10	0.22	0.45	-0.20	1 (18)	Dubious case, discussed in Appendix III
				Ind139	5.46	0.22	0.42	-0.15	2 (18)	2 mismatches
				Ind83	3.38	0.22	0.33	-0.11	3 (18)	3 mismatches
V011	Ind50	2001	S Norway	IndV003	5.69	0.25	0.18	-0.20	1 (16)	CP-O too low
V015	Ind51	2001	S Norway	Ind25	4.27	0.70	0.53	0.52	0 (17)	M-CP too high
				Ind156	3.93	0.70	0.50	0.17	0 (16)	Dubious case, discussed in Appendix III
				Ind165	3.88	0.70	0.44	0.09	0 (14)	Not assigned according to above
				IndV003	3.06	0.70	0.49	0.11	0 (17)	Not assigned according to above
V016	Ind51	2001	S Norway	Ind25	6.51	0.78	0.77	0.52	0 (18)	M-CP too high
R001	Ind57	2004	S Norway	Ind85	4.03	0.64	0.38	0.10	0 (16)	Assigned
R002	Ind57	2004	S Norway	Ind85	5.67	0.36	0.69	0.10	0 (16)	Assigned
				Ind31	5.05	0.36	0.49	-0.21	0 (16)	Other male assigned
V028	Ind89	2004	S Norway	Ind41	6.21	0.39	0.36	-0.40	0 (14)	Assigned
V029	Ind89	2004	S Norway	Ind41	4.38	0.23	0.39	-0.35	1 (16)	Assigned
V024	Ind97	2004	S Norway	-	-	0.53	-	-	-	-
V025	Ind97	2004	S Norway	-	-	0.75	-	-	-	-