Does the spatiotemporal distribution of livestock influence forage patch selection in Eurasian lynx Lynx lynx?

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Depredation on livestock is one of the main conflicts associated with Eurasian lynx *Lynx lynx* conservation in Norway. Our study investigates how Eurasian lynx utilise high-density patches of free-ranging and unguarded livestock (domestic sheep *Ovis aries* and semi-domestic reindeer *Rangifer tarandus*) as compared to patches associated with low-density wild ungulate prey, roe deer *Capreolus capreolus*. We monitored 10 radio-collared lynx in central Norway in two seasons that differed in ungulate distribution and density. According to the 'optimal foraging theory' an animal should preferentially utilise areas with more abundant food if not constrained by other factors; therefore we predicted that lynx should select patches containing livestock. Contrary to our prediction the results indicate no selection for livestock patches in any season. In contrast, a clear preference was shown for roe deer patches in both seasons. Our findings support the hypothesis that lynx depredation on livestock seems to be affected by chance encounter rates, rather than by active selection for livestock-dense patches. We conclude that habitat selection by lynx seemed to be governed by a number of other factors than food alone, and that lynx predation on livestock, especially on sheep, should not be regarded as being ecologically equivalent to predation on wild prey.

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Depredation on livestock is one of the main conflicts associated with the conservation of Eurasian lynx *Lynx lynx* in Europe (Breitenmoser et al. 2000), and especially in Norway where an estimated 5,000-10,000 free-ranging domestic sheep *Ovis aries* are compensated as killed by lynx each summer (Odden et al. 2002). In addition, several thousand semi-domestic reindeer *Rangifer tarandus* are also compensated as killed by lynx (Nybakk et al. 2002). A central prerequisite for the development of any management strategy for lynx is an understanding of the ecology of their depredation on livestock, and how it relates to their normal predation behaviour (Odden et al. 2002).

The availability and distribution of food is considered as the single-most important factor determining social systems and spacing patterns in large carnivore species (Macdonald 1983, Sandell 1989). On a finer scale, prey density and dispersion is also expected to affect the foraging behaviour of individual carnivores (Litvaitis et al. 1986, Powell et al. 1997), e.g the optimal foraging theory (OFT; MacArthur & Pianka 1966). According to OFT it is expected that foraging carnivores should exploit habitat patches that contain the most abundant and thus most accessible prey, unless their movements are constrained by other factors (Sandell 1989). Throughout most of its range in Europe, the Eurasian lynx prefers small and medium-sized ungulate prey, when available (Jedrzejewski et al. 1993). In central Norway three ungulate species occur in significant numbers; one is a wild species, roe deer *Capreolus capreolus*, one is a semi-domestic species, reindeer, and one is a domestic species, sheep. All three species occur in the diet of lynx in the region (Sunde et al. 2000a). The two domestic species occur in predictable and high-density patches, and like most livestock (MacCracken & Hansen 1987, Sacks & Neale 2002) have poorly developed anti-predator behaviour as compared to roe deer. In addition, Norwegian livestock graze freely in forest and alpine-tundra habitats, and are rarely guarded.

In this study, we followed a sample of radio-collared lynx to determine their pattern of habitat patch selection in relation to the composition of ungulate prey available within the patch. Because the density of the wild ungulate prey, roe deer, was relatively low in our study area compared to the two domestic prey species, sheep and reindeer, and the fact that relatively large numbers of livestock are compensated as killed by lynx every year in the region, we predicted that lynx would select patches that contained domestic ungulates.

Material and methods

Study area

Our study area covered the northern part of the county of Nord-Trøndelag and a small area in the southernmost part of the county of Nordland (64°N, 12°E), a total area of 7,405 km² in central Norway. The area bounded by the sum of the minimum convex polygon home ranges of the monitored lynx constituted the boundaries of the study area (Fig. 1). The study area was mainly beneath the alpine-tundra vegetation zone, and was dominated by middle and northern boreal forest vegetation, but with small areas belonging to the southern boreal forest zone (Moen 1998). The topography is dominated by low mountains, and stretches from the coast to a maximum elevation of 1,160 m a.s.l. The tree line occurs at elevations of 300-400 m a.s.l. Boreal coniferous forests with Norway spruce *Picea abies* in various successional stages predominate below the tree line, and most forest areas are logged on rotation. The subalpine belt contains areas of Scots pine *Pinus sylvestris* and birch *Betula pubescens* forest. Agricultural areas are scattered throughout the lowland. Lynx density in the county was estimated to be 0.53/100 km² in January 1996, including dependent cubs (Kvam 1997). Other large carnivores in the study area are wolverines *Gulo gulo* at low densities in the alpine areas, and occasionally dispersing brown bears *Ursus arctos*.

Roe deer are widely distributed in all forested areas during summer, but concentrate in valley bottoms close to agricultural land and human habitation during winter (Sunde 1996). Semi-domestic reindeer herds migrate between different areas throughout the year, predictably spending summers in inland alpine-tundra areas and the winters in forested areas on the coast (Kjelvik et al. 2000). Sheep are patchily distributed during summer in both forest and alpine-tundra habitats. The sheep are not fenced or herded and do not demonstrate clear flocking tendencies. Rather, each ewe and her lambs occupy a home range, although all the sheep belonging to a given owner tend to occupy the same general area resulting in a patchy distribution.

Lynx data collection

The study was carried out from January 1994 through March 1997, when a total of 14 lynx (11 independent individuals and three kittens) were radio-tagged (see Sunde et al. 2000b for further details). Only 10 of these independent lynx individuals were followed long enough to calculate their home range. Lynx were caught in box traps or in padded leg-hold traps placed near kills, and fitted with radio-collars (Nybakk et al. 1996). Whenever
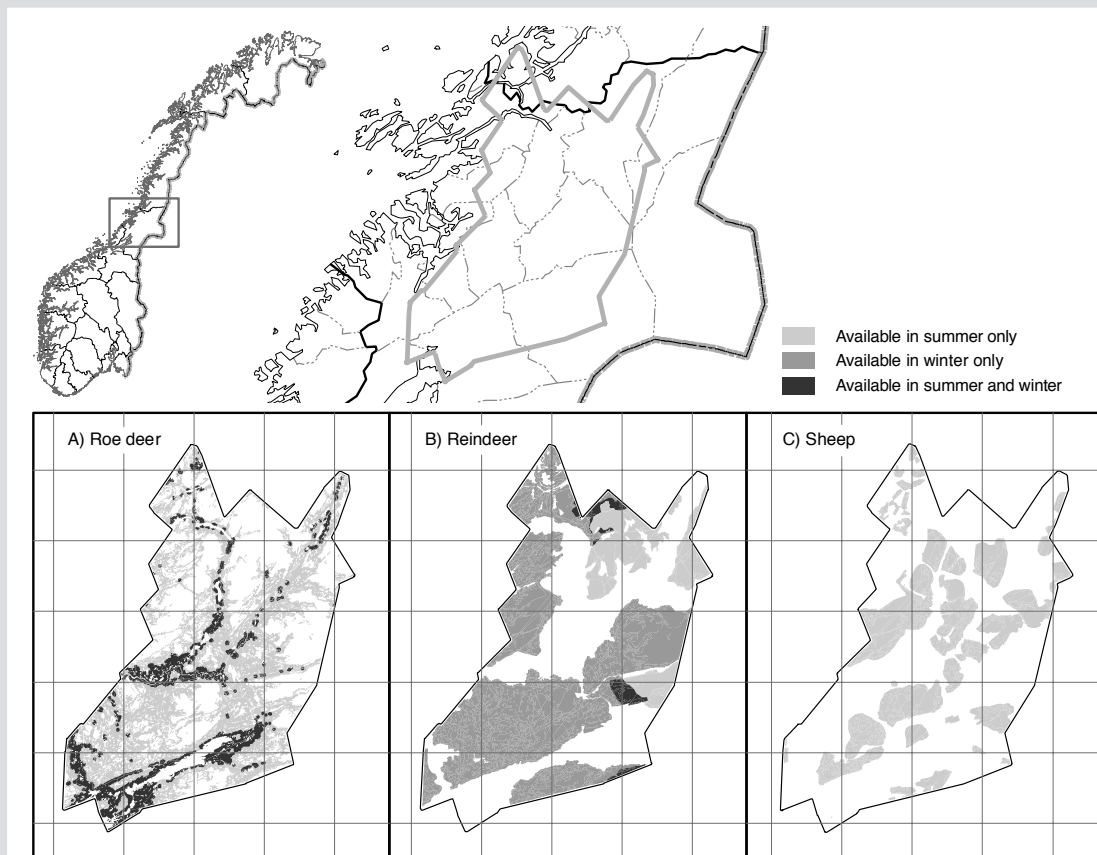
Figure 1. Distribution of the ungulate prey roe deer (A), reindeer (B) and sheep (C) in the study area. The prey was available either in summer only (■), in winter only (■) or in both summer and winter (■). Each grid cell represents an area of 25 × 25 km.

possible, lynx were radio-tracked daily using standard telemetry techniques (see Sunde et al. 2000b). The starting time of the radio-tracking session was chosen at random so that each lynx was triangulated at all hours. Our results therefore give a description of areas used by lynx both during day (resting) and night (roaming and hunting). However, lynx spent most days on a kill and chose day lairs usually within 1 km of a kill (Pedersen et al. 1999, Øvrum 2000), so that most locations should reflect either areas being used for hunting or day lairs in proximity to a kill. We calculated 100% MCP home ranges for each lynx. If a lynx changed status from subadult to adult, we calculated two different home ranges, one for the subadult stage and one for the adult stage, in order to account for dispersal. However, the animal was treated as one individual in the further analyses, even if data were available for more than one year. Only one point per day was used, minimising temporal and spatial auto-

correlation (Harris et al. 1990, De Solla et al. 1999). For information concerning the sample size of locations used to calculate home ranges, seasonal variability in space use, and home range overlap see Sunde et al. (2000b).

Description of ungulate distribution and density

Based on known seasonal habitat associations of roe deer and data provided by sheep farmers and reindeer herders, we created seven data sets, one for each prey species (reindeer, sheep and roe deer) and the four possible combinations between them (Table 1). We investigated lynx habitat use in relation to ungulate distribution in two separate seasons. The winter season (1 January-30 April) was characterised by a reindeer distribution covering a relatively large part of the study area, the roe deer being mainly associated with cultivated land, and sheep being totally absent (kept indoors). The summer season (1 June - 30 September) was characterised by a the reindeer dis-

Table 1. Categorisation of the seven types of ungulate patches available in the study area. Areas defined as 'no ungulate prey patches' comprised 40 and 22% of the study area in the winter and summer seasons, respectively.

Type of patch		Description	Part of study area in summer (s) and winter (w)	Part above the tree line in summer (s) and winter (w)
1	Reindeer	The areas were defined in accordance with information from the reindeer herding authorities. The areas were mostly near the coast or at lower altitudes in winter and at inland areas at higher altitudes in summer.	s: 48% w: 8%	s: 60% w: 17
2	Sheep	The areas were defined based on information from the municipal agricultural authorities. Sheep were released on grazing areas in May/June, mainly in the forested parts of the areas. Sheep foraged successively in higher parts of the grazing areas until gathering in September.	s: 15% w: 0%	s: 26%
3	Roe deer	The areas were defined following the distribution described by Sunde (1996): Summer; all forested and agricultural areas. Winter; all agricultural areas and all forested areas closer than 1 km to agricultural areas.	s: 37% w: 10%	
4	Reindeer and sheep	Part of the study area where reindeer and sheep areas overlap.	s: 1% w: 0%	
5	Reindeer and roe deer	Part of the study area where reindeer and roe deer areas overlap.	s: 3% w: 2%	
6	Sheep and roe deer	Part of the study area where sheep and roe deer areas overlap.	s: 13% w: 0%	
7	Reindeer, sheep and roe deer	Part of the study area where reindeer, sheep and roe deer areas overlap.	s: 1% w: 0%	

tribution covering a small part of the study area, but the reindeer appeared in relatively high densities within these areas (mainly due to the supply of calves). In addition sheep were available as prey in high-density patches and roe deer were scattered throughout the forested parts of the study area. Parts of four and five separate reindeer grazing areas (administrative units) were located inside the study area in the winter and summer seasons, respectively, whereas 34 separate sheep patches or grazing areas (ranging within 45-482 km^2) were available in the summer season. The density of the three ungulate prey species in question changed noticeably between the seasons, where reindeer densities varied from 1-3 to 3-7 reindeer/km^2 inside the defined grazing areas in the winter and summer seasons, respectively. The sheep densities inside the grazing areas in the summer season ranged within 2-38 sheep/km^2, whereas the roe deer areas contained densities of roughly estimated < 2 roe deer/km^2 in winter (Sunde et al. 2000a).

Analyses of forage patch selection

Within each lynx home range, we randomly distributed 1,000 points, representing the 'availability' of patches, and used radio fixes to describe 'used' patches in a logistic regression model with reindeer, roe deer and sheep as binary explanatory variables in order to calculate a resource selection function for each individual lynx (sampling protocol A in Manly et al. 2002). We ran one logistic regression model for each individual both summer and winter, following the suggestion by Manly et al.

(2002). In such a logistic regression, the parameter estimates represent a relative probability function, making it impossible to calculate the real probabilities. However, since the intercept represents no prey available (0 in all prey classes), the exp (parameter estimate x) represents the odds of using an area of class x compared to no ungulate prey available (Manly et al. 2002). The estimates for each prey class and season were then calculated for each animal in a logistic regression with all prey classes as explanatory variables. In order to test for significant preference (if coefficients are higher than 0) or avoidance (if coefficients are lower than 0) for a prey area, we ran t-tests on pooled estimates for all lynx. All statistical analyses were run in S-plus version 6.0 (Insightful Inc. 2001).

Results

Summer

Of the 10 lynx seven had access to all patch types, and all seven lynx showed a significant selection for roe deer patches (pooled data for all lynx; $\beta = 1.667$, $t = 9.420$, $df = 6$, $P < 0.001$). Furthermore, all but two showed avoidance of reindeer patches, but the pooled data for all lynx indicated no selection or avoidance for such patches (pooled data for all lynx; $\beta = -1.214$, $t = -1.330$, $df = 6$, $P = 0.232$). Also, five lynx showed avoidance of sheep patches, but when pooled, the lynx showed no selection for or against sheep patches ($\beta = -0.379$, $t = -1.328$, $df =$

6, P = 0.232). However, reindeer areas and roe deer patches can be considered as non-overlapping with each other, since reindeer mainly occur in the alpine-tundra habitats, whereas roe deer patches are defined as forested areas. Therefore, we wanted to explore the use of roe deer patches compared to sheep (mainly found in the forest) while excluding reindeer from the analyses. We then consider reindeer patches as 'no ungulate prey' patches, and thereby increased the number of lynx to 10 individuals. In this analysis, all lynx showed a selection for roe deer patches (pooled data for all lynx; $\beta = 1.616$, $t = 10.724$, $df = 9$, $P < 0.001$), and no general pattern of selection for or against sheep patches (pooled data for all lynx; $\beta = -0.193$, $t = -0.811$, $df = 9$, $P = 0.439$). A paired t-test showed a significant difference between the selection for roe deer patches and sheep patches among the 10 individuals (mean difference (roe deer - sheep) = 1.809, $t = 6.537$, $df = 9$, $P < 0.001$).

Winter

All lynx had both reindeer and roe deer patches available within their home ranges during the winter season. There was a selection for roe deer patches among all but one lynx (test for all lynx; mean $\beta = 1.118$, $t = 3.844$, $df = 9$, $P = 0.004$). No selection was found for reindeer patches, and eight lynx showed an avoidance of such areas. However, the t-test of all lynx pooled only indicated a trend of avoidance (mean $\beta = -2.270$, $t = -1.972$, $df = 9$, $P = 0.080$). The selection for roe deer patches was significantly different (higher) than for reindeer patches (paired t-test, roe deer areas - reindeer areas; mean difference = 3.389, $t = 2.850$, $df = 9$, $P = 0.019$).

Individual values concerning the availability vs the use of different ungulate patches at the home range level in both seasons, are given in Appendix I.

Discussion

Contrary to our prediction the results indicate no selection for livestock patches in any season. In contrast, a clear preference was shown for roe deer patches in both seasons, although winter patches with reindeer and summer patches with sheep covered relatively large parts of the study area, and both prey species occurred in considerably higher densities than roe deer in the study area. Various hypotheses could possibly explain this lack of selection for livestock patches: 1) the livestock patches are unsuitable as lynx habitats, 2) a greater level of human activity, including risk of human-induced mortality, inside vs outside livestock patches, 3) the importance of wild prey (mainly roe deer) as a reliable prey base in deter-

mining lynx social organisation, and 4) the ontogeny of search images and prey recognition concerning livestock.

According to hypothesis 1, these findings may be explained on the basis of the general lynx preference for the forested parts of the study area (Sunde et al. 2000b), resulting in lynx and roe deer having similar habitat preferences (see also Stahl et al. 2001). But it is hard to imagine that similarity in habitat preferences alone could explain our findings, as 75% of sheep grazing areas were also found below the tree line. It is also hard to imagine that potential habitat differences concerning cover and resting places, between grazed and ungrazed forest areas, could play an important role in explaining the preference for roe deer patches (see Stahl et al. 2002, for a discussion of the importance of different habitat features for sheep depredation risk). Differences in habitat preferences could, however, help to explain the lack of preference for reindeer patches. Even though a considerable amount of the defined reindeer grazing areas were also below the tree line, investigations have shown that semi-domestic reindeer prefer the alpine part of the grazing areas (Landa et al. 2001).

Could the level of human activity inside vs outside the livestock patches (hypothesis 2), explain our findings? Herfindal (2000) documented that a higher level of human activity (density of roads and housing) was associated with lower sheep killing rates by lynx, in southern Norway. In addition, almost all documented adult lynx mortality in the study area was human induced (hunting and traffic accidents; Sunde et al. 1998). Preliminary analyses indicate no higher density of roads and housing inside these livestock patches vs outside (P. Moa, unpubl. data). As the livestock guarding intensity was also very low in these large patches, we find it hard to believe that this element alone could explain why lynx did not use these patches as expected. However, even if it is hard to demonstrate a clear connection between livestock patches and lynx mortality today, it is a possibility that this connection lies in the past, i.e. in the first half of the twentieth century when the population went through a human caused bottleneck (Kvam 1998). Norwegian lynx may have been exposed to a strong selection against killing livestock, if a considerable number of the lynx killed during that period were associated with livestock depredation.

The preference for patches containing roe deer in our study area may also reflect the importance of a reliable prey base (hypothesis 3). According to the social organisation that is predicted for solitary carnivorous mammals (i.e. intra-sexual territoriality secures females' access to prey resources and males' access to females; Sandell

1989), it is reasonable to believe that relatively resident roe deer are of greater importance in determining territory placement for adult female lynx, than migratory reindeer and seasonally available sheep. If this social organisation is mainly established in the winter season, when food access is expected to be at the lowest level (Sandell 1989), and maintained in the same way in the study area in the summer season (Sunde et al. 2000b), roe deer will be the only relatively reliable ungulate prey to take into account.

Although both semi-domestic reindeer and domestic sheep basically are regarded as livestock, there are obvious differences between them, mainly because reindeer are available year round as potential prey, whereas sheep are only available during summer. Lynx diet analyses both from the study area in central Norway (Sunde et al. 2000a) and from southeastern Norway (Odden et al. 2002), have shown that sheep rarely constitute a very important part of lynx diet compared to reindeer and/or roe deer. Øvrum (2000) further showed that lynx, if undisturbed, also had a considerably lower utilisation of sheep carcasses compared to carcasses of wild ungulates. The lesser impact of lynx on sheep in relation to roe deer and reindeer, may be dependent on the ontogeny of prey choice behaviour concerning this prey (hypothesis 4); see Murdoch (1969) and Murdoch & Oaten (1975) for a general discussion. As Odden et al. (2002) pointed out: since nearly all sheep are indoors when kittens begin hunting with their mothers in late autumn and winter, lynx will have little chance to establish a search image for sheep until after independence at 11 months of age.

These findings are also supported by results obtained from the use of mortality-sensing radio-collars on sheep and reindeer in our central Norwegian study area. In these studies lynx predation on reindeer (with a predation peak in the calving season and late autumn/early winter) was significant (Nybakk et al. 2002) compared to corresponding predation on sheep (Kvam et al. 1999). Even if lynx are responsible for a considerable number of sheep kills at a national level, as illustrated by the statistics from the 1995 grazing season, when a total of 8,593 sheep were compensated as lynx killed (note that only 650 of these kills were confirmed as lynx-kills, the rest were assumed to be lynx kills; Norwegian Ministry of the Environment 2003), when these numbers are recalculated as 'number of sheep kills per estimated Norwegian lynx individual', they constitute a remarkably small number compared to other large sheep killing carnivores in Norway (see Wabakken 2001).

In conclusion, our results indicate no selection for livestock patches in any season. In contrast, a clear preference was shown for roe deer patches in both seasons. Our findings support the hypothesis that lynx depredation on livestock (especially sheep) seems to be affected by chance encounter rates (Linnell et al. 1999, Stahl et al. 2001, Odden et al. 2002). It appears that especially sheep are mainly killed during chance encounters when performing other activities (e.g. maintaining of territories or hunting for wild prey), rather than being actively selected. Whether this is due to ontogenetic processes associated with the development of search images and prey recognition or constraints associated with social organisation, possibly with evolutionary anti-livestock killing processes as supplementary explanations, remains to be seen.

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Appendix I.

Percentage distribution of randomly distributed points (available) and radio fixes (used) within each lynx home range (se text for details). The upper number in each row gives summer values and the lower number gives winter values for individual lynx. FA = female adult, FS = female subadult, MA = male adult, MS = male subadult.

Patches

Lynx no	Status	Reindeer Available	Reindeer Used	Sheep Available	Sheep Used	Roe deer Available	Roe deer Used	Reindeer/sheep Available	Reindeer/sheep Used	Reindeer/roe deer Available	Reindeer/roe deer Used	Sheep/roe deer Available	Sheep/roe deer Used	Reindeer/sheep/roe deer Available	Reindeer/sheep/roe deer Used	Without ungulate prey Available	Without ungulate prey Used
1	FA	1.3	0	18.8	5.9	36.1	41.2	6.1	0	0	0	25.2	47.1	0.2	0	12.3	5.9
		13.6	11.3	-	-	18.2	34.5	-	-	2.0	17.9	-	-	-	-	66.3	36.6
2	FS	0.7	0	15.1	2.5	48.0	82.5	0	0	0.3	2.5	9.8	10.0	0	0	26.1	2.5
		53.2	7.0	-	-	14.9	50.7	-	-	3.0	8.5	-	-	-	-	28.9	33.8
3	FA	7.8	4.9	3.9	0	51.5	72.1	5.7	3.3	1.7	6.6	9.3	4.9	2.0	0	18.5	8.2
		11.1	7.4	-	-	9.7	14.8	-	-	0.8	0	-	-	-	-	78.4	77.8
4	MA	4.1	2.6	16.1	0	42.1	74.4	0	0	1.7	0	18.1	15.4	0	0	17.9	7.7
		57.8	0	-	-	11.3	50.0	-	-	2.8	0	-	-	-	-	28.1	50.0
5	FA	0	0	17.5	3.0	30.6	57.6	0	0	0	0	11.9	21.2	0	0	40.0	18.2
		50.3	43.5	-	-	4.2	4.4	-	-	2.0	17.4	-	-	-	-	43.6	34.8
6	FS	19.1	12.9	15.2	9.7	25.0	48.4	15.3	1.6	1.0	0	13.6	17.7	1.3	4.8	9.5	4.8
		2.7	0	-	-	6.2	40.0	-	-	0.3	0	-	-	-	-	90.8	60.0
	FA	1.2	2.8	15.7	2.8	25.9	50.0	0.1	0	0	0	16.5	19.4	0	0	40.6	25.0
		53.9	50.0	-	-	3.3	0	-	-	6.4	35.7	-	-	-	-	36.4	14.3
8	FS	0.9	0	18.4	2.6	41.5	63.2	2.0	0	0	0	19.9	34.2	0	0	17.3	0
		50.5	7.1	-	-	15.4	35.7	-	-	2.8	0	-	-	-	-	31.3	57.1
	FA	0	0	0.5	3.1	71.8	65.6	0	0	0	0	4.3	31.3	0	0	23.4	0
		54.1	30.0	-	-	27.5	30.0	-	-	5.7	10.0	-	-	-	-	12.7	30.0
9	MA	13.0	1.9	19.6	9.6	29.6	57.7	3.9	3.6	1.6	1.9	14.5	15.4	0.2	0	17.8	9.6
		39.3	32.1	-	-	7.9	11.3	-	-	1.3	3.8	-	-	-	-	51.4	52.8
10	MA	0	0	17.2	8.8	43.2	44.1	0	0	0	0	24.5	44.1	0	0	15.1	2.9
		62.2	29.0	-	-	13.7	35.5	-	-	3.1	3.2	-	-	-	-	21.1	32.3
13	MS	54.9	0	21.8	18.2	39.1	45.5	0	0	0	0	21.7	27.3	0	0	17.4	9.1
			0	-	-	14.1	69.2	-	-	2.5	0	-	-	-	-	28.5	30.8