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A case study of seasonal, sexual and ontogenetic divergence in the feeding behaviour of the moose (*Alces alces* LINNÉ, 1758)

Short title Sexual segregation in moose

Abstract We examine differential feeding behaviour in a sexual dimorphic ungulate, the moose (*Alces alces* LINNÉ, 1758). Due to different energetic requirements of males and females, as well as between ontogenetic stages (juvenile, subadult, adult), we expect individuals to select forage according to their needs: either for quality or quantity. The selectivity should be less pronounced in winter as forage then is less abundant. To determine forage quality in terms of the amount of abrasive components, we apply the mesowear method of dietary evaluation. We find that male and female moose of all age classes have a similar winter diet. In summer, juvenile female have the least abrasive diet, while adult females feed on more abrasive food than males. With increasing age, males include larger proportions of higher quality food into their diet. This may result not from a differential selective pressure on young males, but from size and quality of their home range, which is supposed to increase with their age.

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Introduction

The differential use of space by males and females outside the breeding season is termed sexual segregation (BowYER 2004) and occurs across taxa such as carnivores or ungulates. There has been confusion about the definition of sexual segregation, since segregation can occur in at least three ways: spatially, socially and by habitat. Causes and consequences of sexual segregation have been topic of researches for more than 40 years now, but we still gain new insights into this field of animal biology. Studies on several ungulate species have shown that sexual segregation often leads to differential habitat use, which may result in remarkable differences in forage selection of the two sexes. This phenomenon has been referred to as "ecological segregation". CONRADT (2005) and RUCKSTUHL (2007) argued that sexual differences in microhabitat use and thus differences in the dietary regimes should better be described as "sexual divergence". In our study we will focus on this divergence.

We use the swedish moose (*Alces alces*) as a test case for a dimorphic ungulate displaying spatial segregation. The moose is the largest member of the family Cervidae and inhabits northern forest across Eurasia (Scandinavia to Russia) and North America (Alaska to Nova Scotia). In Sweden, they primarily feed on willows (*Salix* LINNÉ spp.), Scots pine (*Pinus sylvestris* LINNÉ), rowan (*Sorbus aucuparia* LINNÉ) and aspen (*Populus tremula* LINNÉ), for winter food. In summer, they also include different herbs and deciduous browse species as, common juniper (*Juniperus communis* LINNÉ) into their diet (CEDERLUND et al. 1980). Rut takes place in autumn (CEDERLUND & SAND 1994). Males and females are solitary and use large, distinct homeranges and do seldom meet outside the rut. Previous studies found no differences in habitat quality between the sexes (MIQUELLE et al. 1992), but different preferences in habitat use (CEDER-LUND & OKARMA 1988; MIQUELLE et al. 1992; OLOVSSON 2007) and homerange size (CE-DERLUND & SAND 1994).

Whether this differential habitat use leads to differential feeding behaviour is the focus of this study. We subsequently propose to test divergence of males and females as well as different ontogenetic stages of both sexes in the dietary signal.

As these differences not only occur between males and females, but also within one gender between age classes, we propose that moose should also forage selectively, due to changing energetic requirements during specific life stages. Consequently we included individuals of different age classes into our research design, ranging from yearlings to fully-grown adults. We grouped them into three age classes which represent juveniles, subadults and adults. Four hypotheses concerning foraging activity were tested using the dental mesowear method of dietary evaluation.

Selective foraging does not only depend on individual needs, but also upon availability of forage items. Scandinavian moose inhabit a highly seasonal environment with abundant high-quality food during summer months but more restricted forage availability during winter, as their habitat then is usually covered by snow. Limited food resources in winter and unlimited resources in summer could lead to a situation, that no "sexual divergence" would be observed, because winter depression does not allow for selectivity, while summer superfluous would not deem for selectivity. We therefore propose to test the following hypothesis (H1):

There is no difference between male and female moose of the same age class nor between age classes in dietary composition during winter months.

Size dimorphism is closely related to sexual segregation (MYSTERUD 2000, RUCK-STUHL & NEUHAUS 2002, BOWYER 2004), because higher body-mass leads to higher energy requirements and larger ruminal capacity to higher biomass intake in males (BE-IER 1987, BOWYER 1984, BARBOZA & BOWYER 2000). When reaching sexual maturity, males and females are exposed to different stress situations. While males loose much weight during rut because they stop foraging and expend much energy in fights, females experience rising energy demands during lactation. As juvenile moose do not significantly differ in size during their first year of life and they furthermore are sexually immature we propose to test the following hypothesis (H2): *There is no difference between juvenile male and female moose in dietary composition during the summer when food is .in superfluous.*

According to SAND & CEDERLUND (1996), about one third of subadult moose (1.5–2.5 years) are sexually mature. Consequently they experience stress situations as described above (rut, lactation) and size-dimorphisms becomes more pronounced. We therefore expect males to compensate their rising energy demands by an increased intake of biomass, including also abrasive, fibre-rich plants. Females in lactation, on the other hand, should undergo a change in energy and especially protein requirement. Due to their smaller ruminal capacity we expect them to fulfil their demands by foraging more selectively on high-quality (less rich in fibres and less abrasive) plant components which are rich in protein and easily digestible. Given that not all moose reproduce in their second year, we put foreword the following hypothesis (H₃):

There is a slight difference between subadult male and female moose in dietary composition during summer. While females consume less abrasive forage, males should also include more abrasive plants into their diet.

In the highest age class, all individuals have reached maturity. We therefore expect the trend proposed in H₃ to be more distinct and propose to test the following hypothesis (H₄):

There is a pronounced difference between adult male and female moose in dietary composition (during summer). While females consume less abrasive forage, males also include more abrasive plants into their diet.

Material and Methods

All specimens used are curated at Naturhistoriska riksmuseet (Natural History Museum) Stockholm, Sweden. Overall, 95 individuals were sampled, 43 females and 52 males. All specimens were wild-ranging moose which were shot in southcentral Sweden at Grimsö Wildlife Research Station or surrounding woods. The sampling areas are geographically close and do not differ in habitat structure. Since individual age was not recorded or unknown for the majority of specimen, we applied a system of age classes (CoA) based on post-canine tooth eruption state to all specimens investigated. Specimens were counted as juvenile (CoA1) when upper and lower M3s were not yet erupted through the cortex of the mandibular/maxillary bone. With beginning eruption of one or both upper and/or lower M3s respectively, individuals were counted as subadults (CoA2) until all four M3s were completely erupted and in early wear. Specimens with upper and/or lower M3s in complete and advanced wear were counted as adults (CoA3).

From the few detailed individual age records we can estimate the following time spans corresponding to to the age class system as described above:

CoA1 ranging from 0-1.5 years, CoA2 ranging from 1.5-2.5 years and CoA3 ranging from $2.5 - \infty$, while 16 years was the highest recorded age.

The mesowear method

Museum specimens were carefully cleaned where needed, and a negative mold of the occlusal aspect was made using PROVIL novo Putty regular set (Heraeus Kulzer, Hanau, Germany) polysiloxane dental molding putty. Subsequently, positive casts of the teeth were produced by filling the molds with epoxy resin Injektionsharz EP (Reckli-Chemiewerkstoff, Herne, Germany).

The mesowear method of dietary analysis is based on facet development of check tooth occlusal surfaces. The degree of facet development reflects the relative proportions of tooth-to-tooth contact (attrition) and food to tooth contact (abrasion). Attrition creates facets while abrasion obliterates them. The entire surface of the teeth is affected by tooth wear but mesowear analysis has focused on the buccal cutting edges of the enamel surfaces where the buccal wall (ectoloph) meets the occlusal surface. The mesowear method treats ungulate tooth mesowear as two variables: occlusal relief and cusp shape.

Here we use a new scoring system for mesowear which extends the published protocol (FORTELIUS & SOLOUNIAS 2000) by intermediate stages (Tab. 3). While the conventional scoring convention has two different occlusal relief scores (low and high), we introduce two intermediate stages, which allow a far more subtle resolution. Additional

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scores are high-high (hh) to accommodate strikingly high reliefs with a valleys angle <=90°. The score of high-low (hl) was introduced to accommodate intermediate wear stages between the classical scores of high and low. Cusp shape parameters were extended by two additional scores besides of the conventional scores of sharp, round and blunt. The round-sharp (rs) attributes to cusps with a slightly rounded apex. Round-sharp is scored when a cusp is sharp seen with the naked eye, but rounded when seen through a hand lens. The score round-round (rr) accommodates intermediate stages between the conventional scores round and blunt. Round-round classifies a not yet blunt cusp, the height of which at the highest point is half as long (or shorter) as length of the rounded cusp. This new scoring convention is easy to learn, once one is accustomed to the conventional scoring system, but allows a far better resolution of mesowear, when both, new occlusal relief and new cusp shape scores are combined (Tab.3) Consequently we establish a combined mesowear score, which represents the degree of abrasional contacts involved in the formation of the mesowear equilibrium. A score of 1 being the less abrasion dominated hh/s and a score of 17 represents the most abrasion dominated l/b with 15 intermediate stages. Combining extended scores for occlusal relief and cusp shape results in a high resolution multi step continuum reflecting subtile stages of the mesowear equilibrium without the need of having to deal with shape templates as suggested by RIVALS et al. (2009). The shortcomings of template patterns in mesowear evaluation is clearly seen in their sensitivity to phylogenetic signal and community bias, which must be omitted.

We investigated only permanent upper post canine dentitions, because up to now, there is no consistent comparative mesowear dataset available for the lower jaw dentition. Unworn teeth and teeth in early wear (occlusal surface not yet entirely exposed to wear) were excluded from this study, because when too little wear is involved, no stable mesowear equilibrium can be established in the early stages of tooth wear. Also, dental specimens in very late wear were excluded as suggested by FORTELIUS & SOLOUNIAS (2000). We used left maxillaries preferably, but if the teeth were damaged, right maxillaries were consulted. Following feasibility tests on three extant ruminant species (FRANZ-ODENDAAL & KAISER 2003) and the procedure applied to giraffes (CLAUSS et al. 2007a) and other extant free ranging and captive ruminants (KAISER et al. 2009), the first, second and the third molars were scored. We only included the sharpest to the two cusps of a cheek tooth, in order to be consistent with the comparative data by FORTELIUS & SOLOUNIAS (2000).

Results

Mesowear scores

Male moose of all ages show similar scores during summer month. While the score calculated for juvenile male moose (CoA1, score 5.0), the score for subadult males declines to 4.604 in CoA2. The lowest score for males was detected in the oldest age class (CoA3) with a score of 4.405. With a score of 2.0, young females moose (CoA1) scored much lower than young males or older females. A continuing rise in the score for older females can be observed. Subadult females (CoA2) scored 4.813 and thus slightly higher than males within the same age class, whereas the oldest females even scored much higher than males of the same age (CoA3, score 5.768).

There is no significant difference neither within nor between age classes during winter months. Likewise no difference between sexes was detected. The lowest score was found for males of CoA1 and females of CoA2 (5.472), while the highest score with 5.503 lay just 0.031 points higher (for females of CoA3).

Discussion

Testing the hypotheses

In hypothesis 1 (H1) we proposed that there is no difference between male and female moose of the same age class nor between age classes in dietary composition during winter months. This is in accordance with the observed data. During winter months all individuals show similar scores and hence a similar composition of diet, indicating equal levels of abrasiveness in food quality. We conclude that this might be due to a general limitation in food availability. As no selectivity is possible, all individuals feed on the same type of plants. Higher mesowear scores indicate that the winter diet of moose is overall more abrasive than the summer diet. Therefore we accept H1.



Fig.1 Mesowear scores according to sex and age classes during winter (a) and summer (b) months.

In hypothesis 2 we proposed to find no difference between juvenile male and female moose in dietary composition during the summer when food is in superfluous. Mesowear scores indicate a contrary result. During summer months, juvenile females (CoA1) differ significantly from juvenile males and older males and females in their foraging behaviour. As it can be interpreted from the low mesowear scores, their diet contains a larger amount of browse, respectively higher quality and more easy digestible forage, than those of all other age classes. In comparison, juvenile males include a larger proportion of abrasive food into their diet. With increasing age males constantly include a larger quantity of high quality food (less abrasive browse) into their diet. This is an opposing trend to older females as their diet becomes more abrasive with increasing age. Therefore we reject H2 because we found major differences between forage composition of female and male juvenile moose.

In H3 we expected subadult females to consume less abrasive forage during summer months in order to increase reproductive success. Actually the difference between abrasiveness of diets is marginal for male and female subadult moose. In contrast to our expectations, both feed on a more abrasive diet than juvenile females do. Generally, fecundity is strongly and positively correlated to individual traits such as age and body size in female ungulates (SADLEIR 1969, WHITE 1983, REIMERS 1983, SÆTHER & HAAGENRUD 1983, 1985; Albon et al. 1983, Gaillard et al. 1992, Sand 1996). Though energy reserves that are invested in reproduction cannot be used for further growth, early reproduction seems to increase life-time fecundity. It thus seems that female moose undergo selection for early sexual maturity by various agents. This may be due to hunting pressure, as the moose is an important game species in Fennoscandia and populations are almost entirely controlled by man (LYKKE 1974). Due to the short life expectancy, predictability of environmental qualities is low for adults and any delay in reproduction is not likely to be regained later (GEIST 1974, 1977, SCHAFFER 1974, HIRS-FIELD & TINKLER 1975, HASTINGS & CASWELL 1979, SÆTHER & HAAGENRUD 1985). NUTritional quality and digestibility of food plants add to increment in weight an early maturation (HAMILTON & BLAXTER 1980, BLAXTER et. al 1981, LANGVATN et al. 1994) and could explain, why especially young females seem to select for particularly high quality forage (as indicated by low abrasiveness) which generally is considered comparatively rich in protein (CLAUSS et al. 2007). Subadult females do not seem to underlie the same selection as they have already reached maturity and gained reserves. In conclusion we reject H₃.

Finally in H4 we formulated to find a pronounced difference between subadult male and female moose in dietary composition (during summer), with females consuming less abrasive forage and males also including more abrasive plants into their diet. Mesowear scores show that those adult females examined in our study did not exhibit such selective foraging behaviour. Several reasons may contribute to this. Firstly, energy demands rise extremely during lactation (at the peak of lactation 2.5–5 times

higher than demands of a non-reproductive female; CLUTTON-BROCK 1991). Such an increase may not allow reproducing females to be selective. Secondly, mobility of females with calves is comparatively restricted, making them more dependent on the resources of a relatively save local environment. This in turn would allow for less selectivity in their foraging behavior. Therefore we reject H4.

Results indicate that males underlie a different if not opposing selection pressure. In comparison to juvenile females, juvenile male moose include a larger amount of abrasive forage into their diet. With increasing age the proportion of high-quality forage increases as it does in females. On the one hand, this must be due to a different behavioural mechanism. Male moose show differential territorial behaviour of subadult and adult males (CEDERLUND & SAND 1994). During rut, younger individuals occupy much smaller home ranges than older, larger males (CEDERLUND & SAND 1994). In general, there is more likelihood that smaller territories contain a more limited resource of high quality browse as compared to larger territories. Furthermore, older males invest more energy in reproductive efforts because their prospects of success are higher compared to young, small-antlered males (CLUTTON-BROCK 1982, SCHWARTZ et al. 1982, BOWYER 1986). This results in young males loosing less weight during their first rut compared to older individuals (CEDERLUND & SAND 1994). However, practicing selective foraging for high energy food would not allow a young male to achieve sufficient increase in body weight to out-compete a long-established, older male on a short term. We conclude that a rapid increment in weight/body-size is not correlated with higher reproductive success in males as it is in females.

If this hypothesis is correct, our data should indicate a tightly balanced behavioral system in the moose, which previously was not recognized as to display sexual segregation in its foraging behavior and habitat needs.

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Tables

			Ν			
	class of age (CoA) 1	class of age (CoA) 2		class of age (CoA) 3		total
female	9	10		24		43
male	6	15		31	l	52
						95

Tab.1 Data composition and sample size.

Tab.2 Calculated mesowear scores for male and female moose.

gender	class of age (CoA)	winter months (oct-mar)	summer months (apr-sep)
female	1	5,47552448	2
	2	5,47192982	4,8125
	3	5,50347222	5,76785714
male	1	5,47192982	5
	2	5,46977547	4,60416667
	3	5,46655232	4,4047619

$\ensuremath{\mathsf{Tab.3}}$ Combinations of refined mesowear variables and resulting scores.

occlusal relief cusp shape	hh	h	hl	hh	h	hl	hh	h	hl	h	hl	l	l	l	l	hl	l
	S	s	S	rs	rs	rs	r	r	r	rr	rr	S	rs	r	rr	b	b
mesowear score	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17

Tab.4 Original Mesowear data and specimens included in the study.

id	sex	tooth	side	occlusal relief	cusp shape anterior	cusp shape posterioir	class of age (CoA)
NRM-581262	male	txM1	left	h	_	rs	3.0
NRM-581262	male	txM2	left	h	_	S	3.0
NRM-581262	male	txM3	left	hh	rs	r	3.0
NRM-587714	female	txM1	left	h	rs	rs	3.0
NRM-587714	female	txM2	left	h	rs	_	3.0
NRM-587714	female	txM3	left	_	-	_	3.0
NRM-587726	female	txM1	left	h	rs	rs	3.0
NRM-587726	female	txM2	left	h	r	_	3.0
NRM-587726	female	txM3	left	h	_	rs	3.0
NRM-587727	female	txM1	left	h	-	rs	3.0
NRM-587727	female	txM2	left	h	_	S	3.0
NRM-587727	female	txM3	left	h	_	rs	3.0
NRM-587732	female	txM1	left	h	r	S	3.0

id	sex	tooth	side	occlusal relief	cusp shape anterior	cusp shape posterioir	class of age (CoA)
NRM-587732	female	txM2	left	h	rs	_	3.0
NRM-587732	female	txM3	left				3.0
NRM-587748	male	txM1	left	h	rs	rs	3.0
NRM-587748	male	txM2	left	h	_	rs	3.0
NRM-587748	male	txM3	left	h	rs	S	3.0
NRM-587754	female	txM1	left	h	r	rs	3.0
NRM-587754	female	txM2	left	h	r	rs	3.0
NRM-587754	female	txM3	left				3.0
NRM-587758	male	txM1	left	h	rs	rs	3.0
NRM-587758	male	txM2	left	h	rs	rs	3.0
NRM-587758	male	txM3	left				3.0
NRM-587761	male	txM1	left	h	r	r	3.0
NRM-587761	male	txM2	left	h	rs	rs	3.0
NRM-587761	male	txM3	left	h	r	rs	3.0
NRM-587763	male	txM1	left	hh	rs	rs	3.0
NRM-587763	male	txM2	left	hh	_	rs	3.0
NRM-587763	male	txM3	left	hh	r	rs	3.0
NRM-587764	male	txM1	left	h	_	r	3.0
NRM-587764	male	txM2	left	h	_	S	3.0
NRM-587764	male	txM3	left	h	rs	rs	3.0
NRM-587766	female	txM1	left				3.0
NRM-587766	female	txM2	left				3.0
NRM-587766	female	txM3	left				3.0
NRM-587771	female	txM1	left	h	r	rs	3.0
NRM-587771	female	txM2	left	h	r	rs	3.0
NRM-587771	female	txM3	left	h	_	_	3.0
NRM-587772	female	txM1	left	h	_	rs	3.0
NRM-587772	female	txM2	left	h	r	rs	3.0
NRM-587772	female	txM3	left	h	_	S	3.0
NRM-587774	male	txM1	left	h	S	rs	3.0
NRM-587774	male	txM2	left	h	r	S	3.0
NRM-587774	male	txM3	left	h	rs	-	3.0
NRM-587779	male	txM1	left	h	r	rs	3.0
NRM-587779	male	txM2	left	h	r	S	3.0
NRM-587779	male	txM3	left	hh	r	S	3.0
NRM-587782	male	txM1	left	h	-	_	3.0
NRM-587782	male	txM2	left	h	-	rs	3.0
NRM-587782	male	txM3	left	h	_	r	3.0
NRM-587783	male	txM1	left	h	r	r	3.0
NRM-587783	male	txM2	left	hl	r	_	3.0

id	sex	tooth	side	occlusal relief	cusp shape anterior	cusp shape posterioir	class of age (CoA)
NRM-587783	male	txM3	left				3.0
NRM-592853	male	txM1	left	h	_	rs	3.0
NRM-592853	male	txM2	left	h	rs	r	3.0
NRM-592853	male	txM3	left	h	rs	rs	3.0
NRM-592855	male	txM1	left	h	rs	rs	3.0
NRM-592855	male	txM2	left	h	_	rs	3.0
NRM-592855	male	txM3	left	h	rs	rs	3.0
NRM-597268	male	txM1	left	h	_	rs	3.0
NRM-597268	male	txM2	left	h	_	rs	3.0
NRM-597268	male	txM3	left	h	_	rs	3.0
NRM-597521	male	txM1	left	_	_	_	3.0
NRM-597521	male	txM2	left	h	_	rs	3.0
NRM-597521	male	txM3	left	h	_	rs	3.0
NRM-597752	female	txM1	left	h	r	rs	3.0
NRM-597752	female	txM2	left	h	rs	r	3.0
NRM-597752	female	txM3	left	h	rs	rs	3.0
NRM-601801	female	txM1	left	h	rs	rs	3.0
NRM-601801	female	txM2	left	h	_	rs	3.0
NRM-601801	female	txM3	left	h	rs	rs	3.0
NRM-601810	female	txM1	left	h	r	rs	3.0
NRM-601810	female	txM2	left	h	rs	rs	3.0
NRM-601810	female	txM3	left	h	rs	_	3.0
NRM-606008	female	txM1	left	hl	rs	_	3.0
NRM-606008	female	txM2	left	h	r	rs	3.0
NRM-606008	female	txM3	left	h	r	rs	3.0
NRM-607059	female	txM1	left	h	rs	S	3.0
NRM-607059	female	txM2	left	h	rs	rs	3.0
NRM-607059	female	txM3	left	h	_	_	3.0
NRM-710090	female	txM1	left	hl	_	S	3.0
NRM-710090	female	txM2	left	h	_	r	3.0
NRM-710090	female	txM3	left	h	r	rs	3.0
NRM-835202	female	txM1	left	h	rs	rs	3.0
NRM-835202	female	txM2	left	h	rs	rs	3.0
NRM-835202	female	txM3	left	h	rs	_	3.0
NRM-855188	female	txM1	left				3.0
NRM-855188	female	txM2	left	h	rs	rs	3.0
NRM-855188	female	txM3	left	hh	r	rs	3.0
NRM-865018	female	txM1	left	h	rs	_	1.0
NRM-865018	female	txM2	left	_	_	_	1.0
NRM-865018	female	txM3	left	_	_	_	1.0

id	sex	tooth	side	occlusal relief	cusp shape anterior	cusp shape posterioir	class of age (CoA)
NRM-875311	female	txM1	left	h	r	rs	3.0
NRM-875311	female	txM2	left	h	rs	r	3.0
NRM-875311	female	txM3	left	hl	r	rs	3.0
NRM-915127	female	txM1	left	h	r	rs	3.0
NRM-915127	female	txM2	left	h	r	r	3.0
NRM-915127	female	txM3	left	hl	r	rs	3.0
NRM-925123	male	txM1	left	h	-	rs	3.0
NRM-925123	male	txM2	left	h	rs	rs	3.0
NRM-925123	male	txM3	left	h	_	S	3.0
NRM-925156	female	txM1	left	h	rs	rs	3.0
NRM-925156	female	txM2	left	h	rs	rs	3.0
NRM-925156	female	txM3	left	h	-	rs	3.0
NRM-925157	male	txM1	left	h	rs	rs	3.0
NRM-925157	male	txM2	left	h	r	r	3.0
NRM-925157	male	txM3	left	h	rs	_	3.0
NRM-975701	male	txM1	left	h	rs	_	1.0
NRM-975701	male	txM2	left	_	-	_	1.0
NRM-975701	male	txM3	left	_	_	_	1.0
NRM-975702	male	txM1	left	h	rs	_	1.0
NRM-975702	male	txM2	left	_	_	_	1.0
NRM-975702	male	txM3	left	_	_	_	1.0
NRM-975703	male	txM1	left	h	rs	S	3.0
NRM-975703	male	txM2	left	h	rs	_	3.0
NRM-975703	male	txM3	left	h	-	r	3.0
NRM-975704	male	txM1	left	h	r	rs	3.0
NRM-975704	male	txM2	left	h	_	S	3.0
NRM-975704	male	txM3	left	h	_	_	3.0
NRM-975705	male	txM1	left	h	rs	rs	3.0
NRM-975705	male	txM2	left	h	rs	_	3.0
NRM-975705	male	txM3	left	h	_	_	3.0
NRM-975713	female	txM1	left	h	rs	rs	3.0
NRM-975713	female	txM2	left	hh	r	rs	3.0
NRM-975713	female	txM3	left	h	_	rs	3.0
NRM-975715	female	txM1	left	h	rs	S	3.0
NRM-975715	female	txM2	left	h	rs	S	3.0
NRM-975715	female	txM3	left	h	-	-	3.0
NRM-975717	female	txM1	left	h	S	_	1.0
NRM-975717	female	txM2	left	_	_	_	1.0
NRM-975717	female	txM3	left	_	_	_	1.0
NRM-975721	male	txM1	left	h	rs	rs	3.0

	1					1	
10	sex	tooth	side	occlusal relief	cusp shape anterior	cusp shape posterioir	class of age (CoA)
NRM-975721	male	txM2	left	h	s	_	3.0
NRM-975721	male	txM3	left				3.0
NRM-975722	male	txM1	left	h	S	_	3.0
NRM-975722	male	txM2	left	h	s	_	3.0
NRM-975722	male	txM3	left	h	_	_	3.0
NRM-975723	male	txM1	left	h	S	rs	3.0
NRM-975723	male	txM2	left	h	s	_	3.0
NRM-975723	male	txM3	left	h	_	_	3.0
NRM-975724	female	txM1	left	h	rs	_	1.0
NRM-975724	female	txM2	left	-	_	_	1.0
NRM-975724	female	txM3	left	_	_	_	1.0
NRM-975726	male	txM1	left	h	rs	rs	3.0
NRM-975726	male	txM2	left	h	_	s	3.0
NRM-975726	male	txM3	left				3.0
NRM-975728	female	txM1	right	h	rs	_	2.0
NRM-975728	female	txM2	left	_	_	_	2.0
NRM-975728	female	txM3	left	_	_	_	2.0
NRM-975729	male	txM1	left	h	S	_	1.0
NRM-975729	male	txM2	left	_	_	_	1.0
NRM-975729	male	txM3	left	_	_	_	1.0
NRM-975730	male	txM1	left	h	s	_	3.0
NRM-975730	male	txM2	left	h	S	rs	3.0
NRM-975730	male	txM3	left	h	rs	_	3.0
NRM-975731	female	txM1	left	h	rs	rs	2.0
NRM-975731	female	txM2	left	_	_	_	2.0
NRM-975731	female	txM3	left	_	_	_	2.0
NRM-975732	female	txM1	left	h	rs	rs	2.0
NRM-975732	female	txM2	left	_	_	_	2.0
NRM-975732	female	txM3	left	_	_	_	2.0
NRM-975739	male	txM1	left	h	rs	S	3.0
NRM-975739	male	txM2	left	h		s	3.0
NRM-975739	male	txM3	left	h	rs	_	3.0
NRM-975740	male	txM1	left	h	rs	rs	3.0
NRM-975740	male	txM2	left	h	rs	rs	3.0
NRM-975740	male	txM3	left	h	rs	r	3.0
NRM-975748	male	txM1	left	h	_	r	3.0
NRM-975748	male	txM2	left	h	_	r	3.0
NRM-975748	male	txM3	left	h	_	rs	3.0
NRM-975749	male	txM1	left	h	rs	rs	3.0
NRM-975749	male	txM2	left	h	rs	rs	3.0

id	sex	tooth	side	occlusal relief	cusp shape anterior	cusp shape posterioir	class of age (CoA)
NRM-975749	male	txM3	left	h	r	S	3.0
NRM-975753	female	txM1	left	h	rs	_	1.0
NRM-975753	female	txM2	left	_	-	_	1.0
NRM-975753	female	txM3	left	_	_	_	1.0
NRM-975754	female	txM1	right	h	rs	rs	2.0
NRM-975754	female	txM2	left	_	_	_	2.0
NRM-975754	female	txM3	left	_	_	_	2.0
NRM-975755	female	txM1	left	h	r	rs	1.0
NRM-975755	female	txM2	left	_	_	_	1.0
NRM-975755	female	txM3	left	_	-	_	1.0
NRM-975756	male	txM1	left	h	S	rs	2.0
NRM-975756	male	txM2	left	_	_	_	2.0
NRM-975756	male	txM3	left	_	_	_	2.0
NRM-975757	male	txM1	left	h	S	rs	2.0
NRM-975757	male	txM2	left	h	r	rs	2.0
NRM-975757	male	txM3	left	_	_	_	2.0
NRM-975758	female	txM1	left	h	-	rs	1.0
NRM-975758	female	txM2	left	_	_	_	1.0
NRM-975758	female	txM3	left	_	_	_	1.0
NRM-975759	female	txM1	left	h	rs	_	2.0
NRM-975759	female	txM2	left	_	_	_	2.0
NRM-975759	female	txM3	left	_	-	_	2.0
NRM-975760	male	txM1	left	h	rs	rs	3.0
NRM-975760	male	txM2	left	h	rs	S	3.0
NRM-975760	male	txM3	left	h	S	-	3.0
NRM-975761	male	txM1	left	h	rs	S	3.0
NRM-975761	male	txM2	left	h	rs	_	3.0
NRM-975761	male	txM3	left	h	_	_	3.0
NRM-975762	male	txM1	left	h	rs	rs	2.0
NRM-975762	male	txM2	left	h	_	_	2.0
NRM-975762	male	txM3	left	_	_	_	2.0
NRM-975763	male	txM1	left	h	S	rs	2.0
NRM-975763	male	txM2	left	_	_	_	2.0
NRM-975763	male	txM3	left	_	_	_	2.0
NRM-975764	male	txM1	left	h	rs	S	2.0
NRM-975764	male	txM2	left	h	-	_	2.0
NRM-975764	male	txM3	left	-	_		2.0
NRM-975765	female	txM1	left	h	rs	rs	2.0
NRM-975765	female	txM2	left	-	-	_	2.0
NRM-975765	female	txM3	left	-	_		2.0

id	sex	tooth	side	occlusal relief	cusp shape anterior	cusp shape posterioir	class of age (CoA)
NRM-975767	male	txM1	left	h	r	rs	2.0
NRM-975767	male	txM2	left	h	r	_	2.0
NRM-975767	male	txM3	left	_	_	_	2.0
NRM-975768	male	txM1	left	hh	rs	S	2.0
NRM-975768	male	txM2	left	h	_	_	2.0
NRM-975768	male	txM3	left	_	_	_	2.0
NRM-975769	female	txM1	left	h	S	rs	3.0
NRM-975769	female	txM2	left	h	_	S	3.0
NRM-975769	female	txM3	left				3.0
NRM-975771	female	txM1	left	h	rs	S	3.0
NRM-975771	female	txM2	left	h	rs	_	3.0
NRM-975771	female	txM3	left				3.0
NRM-975773	female	txM1	left	h	rs	rs	3.0
NRM-975773	female	txM2	left	h	_	rs	3.0
NRM-975773	female	txM3	left	_	_	_	3.0
NRM-975775	female	txM1	left	h	rs	_	1.0
NRM-975775	female	txM2	left	_	_	_	1.0
NRM-975775	female	txM3	left	_	_	_	1.0
NRM-975777	female	txM1	left	h	rs	_	1.0
NRM-975777	female	txM2	left	_	_	_	1.0
NRM-975777	female	txM3	left	_	_	_	1.0
NRM-975778	male	txM1	left	h	S	_	1.0
NRM-975778	male	txM2	left	_	_	_	1.0
NRM-975778	male	txM3	left	_	_	_	1.0
NRM-975779	female	txM1	right	h	S	_	1.0
NRM-975779	female	txM2	left	_	_	_	1.0
NRM-975779	female	txM3	left	_	_	_	1.0
NRM-975780	male	txM1	left	h	rs	_	2.0
NRM-975780	male	txM2	left	_	_	_	2.0
NRM-975780	male	txM3	left	_	_	_	2.0
NRM-975781	female	txM1	right	h	S	S	2.0
NRM-975781	female	txM2	left	_	_	_	2.0
NRM-975781	female	txM3	left	_	_	_	2.0
NRM-975782	female	txM1	right	h	rs	_	2.0
NRM-975782	female	txM2	left	_	_	_	2.0
NRM-975782	female	txM3	left	_	_	_	2.0
NRM-975784	male	txM1	left	h	rs	S	2.0
NRM-975784	male	txM2	left	_	_	_	2.0
NRM-975784	male	txM3	left	_	_	_	2.0
NRM-975785	male	txM1	left	hh	rs	rs	2.0

id	sex	tooth	side	occlusal relief	cusp shape anterior	cusp shape posterioir	class of age (CoA)
NRM-975785	male	txM2	left	h	_	_	2.0
NRM-975785	male	txM3	left	_	_	_	2.0
NRM-975786	female	txM1	left	h	rs	rs	2.0
NRM-975786	female	txM2	left	_	_	_	2.0
NRM-975786	female	txM3	left	_	_	_	2.0
NRM-975787	male	txM1	left				2.0
NRM-975787	male	txM2	left	h	rs	_	2.0
NRM-975787	male	txM3	left		_	_	2.0
NRM-975788	male	txM1	left	h	rs	rs	2.0
NRM-975788	male	txM2	left	h	_	_	2.0
NRM-975788	male	txM3	left	_	_	_	2.0
NRM-975790	male	txM1	left	h	rs	rs	2.0
NRM-975790	male	txM2	left	h	_	_	2.0
NRM-975790	male	txM3	left	_	_	_	2.0
NRM-975791	female	txM1	left	h	rs	rs	2.0
NRM-975791	female	txM2	left		_	_	2.0
NRM-975791	female	txM3	left	_	_	_	2.0
NRM-975792	male	txM1	left	h	-	rs	2.0
NRM-975792	male	txM2	left	h	_	_	2.0
NRM-975792	male	txM3	left		-	_	2.0
NRM-975793	male	txM1	left	h	rs	S	3.0
NRM-975793	male	txM2	left	h	rs	rs	3.0
NRM-975793	male	txM3	left				3.0
NRM-975799	male	txM1	left	_	rs	_	1.0
NRM-975799	male	txM2	left		-	_	1.0
NRM-975799	male	txM3	left	_	_	_	1.0
NRM-975800	male	txM1	left	h	rs	_	1.0
NRM-975800	male	txM2	left	_	_	_	1.0
NRM-975800	male	txM3	left	-	_	_	1.0
NRM-975803	male	txM1	left	h	rs	rs	2.0
NRM-975803	male	txM2	left	_	_	_	2.0
NRM-975803	male	txM3	left		_	_	2.0

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