

MOOSE ESCAPE BEHAVIOUR IN AREAS OF HIGH HUNTING PRESSURE

Leonid Baskin¹, John P. Ball^{2,3}, and Kjell Danell²

¹Institute of Ecology and Evolution, Leninsky pr. 33, Moscow, 119071, Russia; ²Department of Animal Ecology, Swedish University of Agricultural Sciences, Umeå, SE-901 83, Sweden; ³e-mail: john.ball@szoook.slu.se

ABSTRACT: Although hunters cause more than 80% of moose mortality in some geographic areas, quantitative studies of how moose attempt to escape humans are surprisingly rare. We experimentally disturbed radio-collared moose of known age and of both sexes to study escape behaviour from humans. We found that larger groups of moose made fewer stops between being disturbed and settling down, and that larger groups exhibited a longer path length before quieting. We detected no significant effect of age (a potential measure of survival rate) on escape behaviour. The escape path of males was significantly longer than females even though the linear distance from the site of disturbance to the location where the moose settled down was not significantly different between the sexes. Overall, the escape path of males from the site of disturbance to where they settled down was significantly more tortuous than that of females. Although males are the preferred prey of hunters, the differences in escape behaviour between the sexes also may contribute to why males are more frequently killed by hunters. Thus, in areas with heavy hunting pressure, hunters may be acting as a selective force that favours animals that immediately run away after disturbance by humans. Finally, published evaluations of the use of hunter observations to index moose populations have often reported that considering the size of a hunting group is necessary to improve the accuracy of those data; our analysis suggests an explanation – differences in escape behaviour between the sexes.

ALCES VOL. 40: 123-131 (2004)

Key words: escape behaviour, gender differences, group size, hunters, hunting, moose, movements, predator, reaction distance, selective force, Sweden

Predation has long been considered one of the most important selective pressures on animals in the wild (Treves 2000). It is thus not surprising that ecologists have long studied many different aspects of predator and prey behaviour. For example, the observation that the vigilance of individual prey declines as their group size increases is one of the most frequently reported relationships in the study of animal behaviour (Roberts 1996).

Among prey species in general, various aspects of escape or anti-predator behaviour have been found to vary with a great number of factors including group size

(Hebblewhite and Pletscher 2002), distance to cover (White and Berger 2001), temperature (Fernandez-Juricic et al. 2002), degree of predation risk (Hamilton and Heithaus 2001), experience with predators (Jachner 2001), and the sex of the prey (Magurran and Nowak 1991). Not surprisingly, evolution often has led to prey that are sensitive to the costs and benefits of different anti-predator behaviours under various circumstances (Frid and Dill 2002). Studies of moose (*Alces alces*) also have revealed a variety of anti-predator behaviours, that include standing its ground against wolves (*Canis lupus*, Mech 1970), increasing group

size when foraging further from cover (Molvar and Bowyer 1994), selecting unpredictable sites to give birth (Bowyer et al. 1999), grouping together if predators are present, and increasing vigilance when with active young or when further from protective refugia (White and Berger 2001, White et al. 2001). Franzmann and Schwartz (1998) provide a further overview of anti-predator (and many other) behaviours in North American moose. However, few published studies have quantified the spatial aspects of escape behaviour of moose when confronted by potential wild predators or humans (but see Glushkov 1976 and Andersen et al. 1996).

Hunting is the most important mortality factor of moose in Fennoscandia (e.g., 81–91% of adult mortality; Ericsson and Wallin 2001) because large predators (brown bears, *Urus arctos*, and wolves, *Canis lupus*) are absent over large areas or occur only at very low densities (Swenson et al. 1994, Persson and Sand 1998, Ericsson et al. 2001). Anecdotal reports by hunters and others suggest that there may be individual variation in escape behaviour – some moose use different escape tactics than others. Furthermore, at least in Russia, moose have been reported to exhibit different escape behaviour in areas with low and high hunting pressure (Glushkov 1976). More knowledge on this issue is needed because humans might be acting as a strong selective agent in those areas that have high hunting pressure, and thereby may alter moose behaviour in the long term. Perhaps most importantly, we need to understand escape behaviour if we are to understand and manage the interaction between the human predator and its prey.

Here, we report what is apparently the first quantitative investigation to consider: (1) does escape behaviour from humans differ between the sexes in moose; (2) is there any correlation between age and the

way a given moose attempts to escape; and (3) does group size affect escape behaviour in moose?

METHODS

The study area (~4,000 km²) is just north of Umeå (63°48' N, 20°17' E), in coastal northern Sweden (Fig. 1). Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and birches (*Betula pendula* and *B. pubescens*) are the dominant tree species, and the field layer vegetation is dominated by bilberry (*Vaccinium myrtillus*), lingonberry (*V. vitis-idea*), and heather (*Calluna vulgaris*). The length of the growing season is about 150 days, starting around mid-May; snow normally arrives in early November and persists to the end of April (SNA 1995). Moose density in the study area (as determined by helicopter census and pellet group counts) ranged between 0.7 and 0.9 moose km⁻² (J.P. Ball unpublished data). Predators (other than humans) capable of taking moose essen-



Fig. 1. Map of the study area in northern Sweden where moose were experimentally disturbed to quantitatively investigate the effects of age, sex, and group size on escape behaviour. Umeå is at the southern edge of the study area.

tially are absent (Swenson et al. 1994, Persson and Sand 1998). Moose are hunted heavily in the area and every year about one-third of the population is harvested. More importantly, in this area, hunters account for 81% of all deaths of female moose born and 91% of all male deaths (Ball et al. 1999, Ericsson and Wallin 2001).

Using a dart rifle fired from a helicopter, we immobilized adult and calf moose with a mixture of ethorphine and xylazine hydrochloride (Sandegren et al. 1987) during February to mid-March every year from 1990. Each moose was fitted with a numbered radio collar and small numbered ear tags. Moose were aged using two complementary methods: at marking, we determined their ages using tooth wear and eruption (Skuncke 1949), and if later harvested, we obtained the jaw, sectioned the first molar, and counted the cementum annuli under at least 20x magnification (Sergeant and Pimlott 1959, Fancy 1980, Bubenik 1998).

When good conditions for snow tracking occurred between January and April during the 1996-97 and 1997-98 winters, we conducted controlled disturbance experiments with these known-aged radio-collared moose. For all tests, a single observer (for consistency) first located the moose by radio-telemetry and thereafter the moose (one individual or group of moose) was disturbed in a uniform way (i.e., a slow quiet approach on skis at the same speed from an initial distance of 70-100 m). After the disturbance, the observer followed the movements of the radio-collared moose by radio signals until it settled down (i.e., started to feed, ruminate, lie down, etc.). Then the observer tracked the moose backward in the snow to quantify the escape path taken (and avoid influencing the escape behaviour other than the initial controlled disturbance).

We quantified the group size, and 5 response variables which quantified the

spatial aspects of the moose's escape behaviour (for a group of moose, the centroid of the group was used). These were: (1) the distance the moose ran, trotted, or galloped after the initial disturbance ("Gallop Distance" hereafter); (2) the total distance the moose moved before settling down ("Path Length to Quieting"); (3) the straight line distance from the place where the moose was disturbed to the point where the moose quieted down ("Straight Length to Quieting"); (4) the number of stops the moose made before quieting ("Number of Stops Before Quieting"); and (5) we calculated a simple index of tortuosity ("Tortuosity") by dividing the "Straight Length to Quieting" by the "Path Length to Quieting". Thus, an animal with a perfectly linear escape path would have a Tortuosity Index of 1.0, whereas a moose which travelled in a non-linear fashion after being disturbed would have an index with a much lower value (e.g., 0.3). See Mårell et al. (2002) for additional approaches to quantifying movement.

Indicator Variable Regression (also known as "Dummy Variable Regression"; Kleinbaum et al. 1987, Tabachnick and Fidell 2001) was used to test for the effects of the independent variables (sex, group size, and age) on the dependent variables that described escape behaviour. Indicator Variable Regression is a form of a General Linear Model that is appropriate to a mixture of categorical (e.g., sex) and continuous (e.g., tortuosity) variables (Kleinbaum et al. 1987, Tabachnick and Fidell 2001). The significance factor reported is the additional explanatory value of adding a variable to a model already containing the other two independent variables (i.e., this statistically controls for any correlations among these independent variables; Cohen and Cohen 1983, Kleinbaum et al. 1987, Tabachnick and Fidell 2001). In keeping with standard practices, if and only if the ANOVA for the

overall indicator variable regression (i.e., containing all independent variables) was significant, did we then examine which individual effects (e.g., sex, group size, or age) accounted for this. Statistical analyses were performed with JMP version 4.0.5 (SAS Institute 2000). We report means \pm 1 standard deviation unless otherwise noted.

RESULTS

In total, 29 controlled disturbances were performed (13 males and 16 females, including one cow of unknown age). The average age of the males we studied was 7.5 ± 2.2 years, and that of females 10.9 ± 4.5 years.

The heavy hunting pressure in the study area is perhaps reflected by the rather strong escape responses made by moose to our experimental disturbances. The Gallop Distance was 293 ± 222 m, the Path Length to Quieting was $1,324 \pm 699$ m, and the Straight Length to Quieting was 855 ± 419 m.

Indicator Variable Regression revealed that the distance that moose ran after being disturbed (Gallop Distance) showed no relationship with the independent variables sex, age, or group size (whole model $r^2 = 0.08$, $P = 0.59$), so we did not examine separate effects. In contrast, the overall model with the dependent variable Path Length to Quieting was significant ($r^2 = 0.36$, $P = 0.01$); Table 1 reveals that age was not important, but sex and group size were predictors (larger groups travelled shorter distances before quieting) and females travelled less (1,022m) before quieting down than did males (1,671m).

The overall model testing the explanatory effects of sex, group size, and age on Straight Length to Quieting was not significant (whole model $r^2 = 0.23$, $P = 0.11$), so again we do not consider separate effects. The overall model testing the effects of sex, age, and group size on the Number of Stops Before Quieting was significant ($r^2 = 0.33$,

$P = 0.02$). Here the independent variable that was important was group size (Table 1), with larger groups making fewer stops.

Finally, the model testing the effects of sex, age, and group size on Tortuosity explained nearly half of the observed variation ($r^2 = 0.46$, $P = 0.002$). Here, however, group size and age were not predictors, but sex was a predictor (Table 1). Females exhibited more linear escape paths (mean Tortuosity Index = 0.78) than did males (mean Tortuosity Index = 0.57).

Our analysis did not indicate an effect of age on escape behaviour. In contrast, our analysis revealed that group size was correlated with the Path Length to Quieting (larger groups settled down after travelling a shorter path). Furthermore, as group size increased, the group tended to keep moving (i.e., they made fewer stops). Finally, several important aspects of escape behaviour differed between the sexes. Although when initially disturbed both sexes galloped the same distance (Gallop Distance), and stopped the same linear distance away from

Table 1. ANOVA effect tables from the indicator variable regression on moose (*Alces alces*) escape behaviour in Sweden. The results of the overall ANOVAs that were performed first are given in the text. Significant effects are highlighted in **bold**.

Source	df	Sum of Squares	F Ratio	Prob > F
Path Length to Quieting (m)				
sex	1	2030616.9	5.7058	0.0255
group size	1	1962848.5	5.5154	0.0278
age	1	139210.9	0.3912	0.5378
Number of Stops Before Quieting				
sex	1	18.336596	1.6672	0.2095
group size	1	55.928378	5.0851	0.034
age	1	42.879506	3.8986	0.0605
Tortuosity				
sex	1	0.40314635	19.282	0.0002
group size	1	0.00000142	0.0001	0.9935
age	1	0.04315248	2.0639	0.1643

the initial disturbance point (Straight Length to Quieting), males travelled a greater total distance ($1,671 \pm 227$ m) than females ($1,022 \pm 104$ m) before settling down (Path Length to Quieting), and males did this by moving in a much more tortuous path than did females (Tortuosity Index for males 0.58 ± 0.06 , females 0.78 ± 0.03).

DISCUSSION

Ungulates use a variety of different strategies to escape hunters. Hiding is a special behaviour exhibited by some forest-dwelling ungulates like wild boar and moose under extremely high hunting pressure (Baskin 1976, 1998). Moose also sometimes escape by running to a safe distance and, from there, observe human activities (Glushkov 1976). This type of behaviour has also been reported for musk deer *Moschus moschiferus* (Zaitsev 1983), roe deer *Capreolus capreolus* (Danilkin 1996), reindeer *Rangifer tarandus* (Baskin and Hjältén 2001), and Alpine ibex *Capra ibex* (Krämer and Aeschbacher 1971). Often, animals demonstrate apparently reckless flight when they barely have seen or heard an approaching human. This type of flight behaviour is common under high hunting pressure for reindeer (Baskin and Hjältén 2001) and moose (Glushkov 2002). A more extreme escape behaviour is for the animal to run beyond its home range; e.g., wild camels *Camelus bactrianus* in Mongolia (Przewalsky 1878), European bison *Bison bonasus* in Caucasus at the beginning of the 20th century (Filatov 1912), and American bison *Bison bison* in North America at the end of the 19th century (Roe 1951).

Our finding that the Path Length to Quieting was 1,671 m for males and 1,022 m for females is comparable to the overall mean distance of 1,147 m travelled by moose fleeing skiers and pedestrians in another rather heavily hunted Scandinavian moose population (Andersen et al. 1996). We

were unable to find any published study on a lightly hunted population for comparison.

Our analysis, that revealed the tendency of males to escape by a more tortuous path than females, may have implications for their likelihood of escaping hunters, but also for how moose counts should be performed, and of understanding the potential biases in hunter observations of moose. We suggest that the greater tortuosity of the escape path of males may mean that they are more likely to come into repeated contact with hunters, and thus more likely to be killed. However, compared to females, males are preferentially harvested by Swedish hunters anyway (Ball et al. 1999), so we are unable to separate the magnitude of the effects of these two factors. In northern Sweden, the most common method of hunting is through the use of baying dogs, whereby the moose stands its ground while it is distracted by a barking dog (and is subsequently shot by a hunter sneaking in) or it flees (and hunters stationed around a particular parcel of land may be able to shoot the moose; Ball et al. 1999). Thus, hunting with dogs should provide a selective pressure for moose that flee, rather than hide, to escape harvest. In Sweden, hunting grounds are typically private, with a group of hunters having the right to hunt only on their particular hunting grounds. As a result, moose practicing a strategy of fleeing may escape the chain of shooters and find themselves beyond harvest by a particular group of hunters. Because moose hunting seasons are long (September 1 – December 31), escaping moose often will find themselves in a new area where there is no group of hunters active on the same day. Compared to escaping in a linear fashion, remaining in the same area (and moving in a tortuous path) seems to be a poor strategy because of the scenting ability of the hunter's dogs; nevertheless, our analysis reveals that this is how males

behave (perhaps the result of past selection by native predators). We suggest that, compared to females, males either prefer to keep a pursuing human within their sensory range or males have a stronger tendency to stay within their home range.

Our analysis suggests that if the observations of hunters are used to estimate population parameters, the proportion of males will be overestimated relative to their true fraction in the population (see Ericsson and Wallin 2001, Sylvén 2003 for additional analyses). Furthermore, if the differences between the sexes that we detected are indeed general, these behavioural differences may help to explain why the size of a hunting group often emerges as an important factor in studies that use observations of moose seen per hour and per hunter, to estimate moose numbers (Ericsson and Wallin 2001, Sylvén 2003). We suggest that this may be because relative to smaller groups, larger groups of hunters may overestimate males even more because the same bull may be sighted several times as it circles to remain in the area.

We do not suggest that our controlled disturbance by a skier just after the hunting season precisely reflects the responses of moose to hunters during the hunt. Rather, our aim was to test if age, sex, or group size in moose is associated with differences in how moose attempt to escape from humans, and to do so in an area where humans are the main mortality source (and thus likely are acting as a selective force on moose behaviour). Thus, quantitative variables like the Distance to Quieting, for example, may well differ between the hunting season and the immediate post-hunting period. On the other hand, the qualitative relationships revealed by our analysis (e.g., the differential responses between the sexes and the effect of group size) seem likely to be less temporally variable, although further research is needed to test this proposition.

We suggest moose escape behaviour is also influenced by group cohesiveness: when any group member (which our analysis suggests would often be a female) flees from a predator, so does the entire group. We suggest that moose managers should be aware of possible interactions among group size, hunting party size, and apparent sex ratio if using hunter observations to estimate moose population characteristics. Further research in this area should help clarify these relationships, and we suggest that incorporating escape behaviour of moose in a quantitative manner, as we have done, may be necessary to understand the mechanisms affecting population estimates.

Our analysis provided no evidence of any relationship between age and escape behaviour, but our test of this aspect is not powerful because of sample size limitations. We suggest that future studies on escape behaviours focus on the effects of group size and sex because the age of wild moose cannot be judged from a distance and few studies will have the luxury, as we did, of tranquilizing moose first to determine their age. Having age data is ideal, but our analysis suggests that it is not essential to understand the escape behaviour of moose towards humans.

The behavioural ecology literature suggests two main advantages for grouping in the presence of predators. First, vigilance: many eyes to detect predators (see Williams et al. 2003 and Bednekoff and Lima 1998 for recent overviews). Second, the other major advantage of being in a group comes from risk dilution: the risk to a given animal in a group of 2 is 50%, in a group of 100 animals it is 1% (Hamilton 1971, Treves 2000, Carbone et al. 2003). In accordance with the risk dilution hypothesis, our analysis reveals that moose apparently do feel safer as group size increases, as indicated by shorter travel distances to quieting.

In conclusion, the differential mortality

exerted by hunters may be selecting for moose which employ a strategy of immediate linear flight, or at least run out of sensory contact with a human after disturbance. We suggest that escape behaviour is an under-studied aspect of moose ecology. This is surprising since humans account for over 80% of all moose deaths in Sweden (Ericsson and Wallin 2001), and are thus expected to be a rather strong selective force. Furthermore, understanding escape behaviour may be critical in improving our ability to use hunter observations to estimate moose populations. Specifically, differences between the sexes in escape behaviour may lead to an apparently greater proportion of males being detected in hunter observations. The variation in escape behaviour with group size we detected may explain why the size of a hunting party often emerges as a significant factor in previous analyses that use hunter observations (e.g., Ericsson and Wallin 2001, Sylvén 2003). Based on our analysis, we suggest that quantifying the escape behaviour of moose may lead to a better understanding of the selective force human hunters are exerting on moose populations, and may lead to improvements in using hunter observations to manage moose populations.

ACKNOWLEDGEMENTS

We thank the Swedish University of Agricultural Sciences (grant to Kjell Danell) for financial support for Leonid Baskin during his stay in Umeå, and the Swedish Environment Protection Agency (grants to Kjell Danell and John P. Ball) for financial support. We also gratefully acknowledge the tireless and expert work by our field technicians (particularly Åke Nordström, Eric Andersson, and Nils-Gunnar Andersson) in the moose project, and K. Wallin for his early work in building up the marked moose population for related studies. The enthusiastic co-operation of many

hundreds of moose hunters over more than a decade allowed us to exactly age our moose, and made possible this and many other investigations. We thank T.R. Stephenson, R. Rea, and an anonymous reviewer for comments which greatly improved the manuscript.

REFERENCES

- ANDERSEN, R., J. D. C. LINELL, and R. LANGVATN. 1996. Short term behavioural and physiological response of moose *Alces alces* to military disturbance in Norway. *Biological Conservation* 77:169-176.
- BALL, J. P., G. ERICSSON, and K. WALLIN. 1999. Climate change, moose and their human predators. *Ecological Bulletins* 47:178-187.
- BASKIN, L. M. 1976. Behaviour of Ungulates. Nauka publishers, Nauka, Moscow, Russia.
- _____. 1998. Moose conservation in ecosystems of Eastern Europe. *Alces* 34:395-407.
- _____, and J. HJÄLTEN. 2001. Fright and flight behaviour of reindeer. *Alces* 37:435-446.
- BEDNEKOFF, P. A., and S. L. LIMA. 1998. Re-examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behaviour. *Proceedings of the Royal Society of London Series B-Biological Sciences* 265:2021-2026.
- BOWYER R. T., V. VAN BALLEMBERGHE, J. G. KIE, and J. A. K. MAIER. 1999. Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. *Journal of Mammalogy* 80:1070-1083.
- BUBENIK, A. B. 1998. Evolution, taxonomy and morphophysiology. Pages 77-124 in A. W. Franzmann and C.C. Schwartz, editors. *Ecology and Management of the North American Moose*.

- Smithsonian Institution Press, Washington, D.C., USA.
- CARBONE C., W. A. THOMPSON, I. ZADORINA, and J. M. Rowcliffe. 2003. Competition, predation risk and patterns of flock expansion in barnacle geese (*Branta leucopsis*). *Journal of Zoology* 259:301-308.
- COHEN, J., and P. COHEN. 1983. *Applied Multiple Regression Correlation Analysis for the Behavioral Sciences*. Erlbaum, New York, New York, USA.
- DANILKIN, A. A. 1996. *Behavioral Ecology of Siberian and European Roe Deer*. Chapman and Hall, London, U.K.
- ERICSSON, G., and K. WALLIN. 2001. Age-specific moose (*Alces alces*) mortality in a predator-free environment: evidence for senescence in females. *Ecoscience* 8:157-163.
- _____, K. WALLIN, J. P. BALL, and M. BROBERG. 2001. Age-related reproductive effort and senescence in free-ranging moose *Alces alces*. *Ecology* 82:1613-1620.
- FANCY, S. G. 1980. Preparation of mammalian teeth for age determination by cementum layers: a review. *Wildlife Society Bulletin* 8:242-248.
- FERNANDEZ-JURICIC, E., M. D. JIMENEZ, and E. LUCAS. 2002. Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. *Canadian Journal of Zoology* 80:1212-1220.
- FILATOV, D. 1912. Caucasian bison. *Zapiski imperatorskoi akademii nauk, otdelenie phisiko-matematicheskoe, Series 7, 30:1-40*. (In Russian).
- FRANZMANN, A. W., and C. C. SCHWARTZ, editors. 1998. *Ecology and Management of the North American Moose*. Smithsonian Institution Press, Washington, D.C., USA.
- FRID, A., and L. DILL. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6:11-16.
- GLUSHKOV, V. M. 1976. Some peculiarities of moose behavior that determine hunter's success. In: S.A. Korytin, editor. *Behavior of Hunting Animals. Sbornik nauchno-tekhnicheskoy informatsii* 51-52:51-58. (In Russian).
- _____. 2002. Ecological basis of moose population management in Russia. Thesis. Vsesoyuznyi Nauchnoissledovatel'skiy institut okhotnichego khozyaistva i zverovodstva, Kirov, Russia. (In Russian).
- HAMILTON, I. M., and M. R. HEITHAUS. 2001. The effects of temporal variation in predation risk on anti-predator behaviour: an empirical test using marine snails. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268:2585-2588.
- HAMILTON, W. D. 1971. Geometry of the selfish herd. *Journal of Theoretical Biology* 31:295-311.
- HEBBLEWHITE, M., and D. PLETSCHER. 2002. Effects of elk group size on predation by wolves. *Canadian Journal of Zoology* 80:800-809.
- JACHNER, A. 2001. Anti-predator behaviour of naive compared with experienced juvenile roach. *Journal of Fish Biology* 59:1313-1322.
- KLEINBAUM, D. G., L. L. KUPPER, and K. E. MULLER. 1987. *Applied Regression Analysis and Other Multivariate Methods*. Duxbury Press, Belmont, California, USA.
- KRÄMER, A., and A. AESCHBACHER. 1971. Zum Slachterhalten des Steinwildes (*Capra ibex*) im Oberengadin, Schweiz. *Säugetierk Mitteilungen* 19:164-171.
- MAGURRAN, A. E., and M. A. NOWAK. 1991. Another battle of the sexes - The consequences of sexual asymmetry in mating costs and predation risk in the guppy,

- Poecilia reticulata*. Proceedings of the Royal Society of London Series B-Biological Sciences 246:31-38.
- MÄRELL, A., J. P. BALL, and A. HOFGAARD. 2002. Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks and Lévy flights. *Canadian Journal of Zoology* 80:854-865.
- MECH, L. D. 1970. *The Wolf: The Ecology and Behavior of an Endangered Species*. Natural History Press, Garden City, New York, USA.
- MOLVAR, E. M., and R. T. BOWYER. 1994. Costs and benefits of group living in a recently social ungulate - the Alaskan moose. *Journal of Mammalogy* 75:621-630.
- PERSSON, J., and H. SAND. 1998. Vargen — viltet, ekologin och människan. Svenska Jägareförbundet, Spånga, Sweden. (In Swedish).
- PRZEWALSKY, N. M. 1878. Wild camel. *Priroda I okhota*, 1-2.
- ROBERTS, G. 1996. Why individual vigilance behaviour declines as group size increases. *Animal Behaviour* 51:1077-1086.
- ROE, F. G. 1951. *The North American Buffalo. A Critical Study of the Species in its Wild State*. University of Toronto Press, Toronto, Ontario, Canada.
- SANDEGREN, F., L. PETTERSSON, P. AHLQVIST, and B. O. RÖKEN, 1987. Immobilization of moose in Sweden. *Swedish Wildlife Research Supplement* 1:785-791.
- SAS Institute. 2000. *JMP Statistics and Graphics Guide*. SAS Institute, Cary, North Carolina, USA.
- SERGEANT, D. E., and D. H. PIMLOTT. 1959. Age determination in moose from sectioned incisor teeth. *Journal of Wildlife Management* 23:315-321.
- SKUNCKE, F. 1949. Älgen, studier, jakt och vård. P. A. Nordstedts och Söners Förlag, Stockholm, Sweden. (In Swedish).
- (SNA) Sveriges National Atlas. 1995. *Sveriges National Atlas - Klimat, sjöar och vattendrag*. Bra Böcker, Höganäs, Sweden.
- SWENSON, J. E., F. SANDEGREN, A. BJÄRVALL, A. SÖDERBERG, P. WABAKKEN, and R. FRANZÉN. 1994. Size, trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. *Biological Conservation* 70:9-17.
- SYLVÉN, S. 2003. Management and regulated harvest of moose (*Alces alces*) in Sweden. *Agraria* 371. Doctoral Thesis, Department of Conservation Biology, Swedish University of Agricultural Sciences, Uppsala, Sweden.
- TABACHNICK, B. G., and L. S. FIDELL. 2001. *Using Multivariate Statistics*. Fourth edition. Allyn and Bacon, Needham Heights, Massachusetts, USA.
- TREVES, A. 2000. Theory and method in studies of vigilance and aggregation. *Animal Behaviour* 60:711-722.
- WHITE, K. S., and J. BERGER. 2001. Antipredator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity? *Canadian Journal of Zoology* 79:2055-2062.
- _____, J.W. TESTA, and J. BERGER. 2001. Behavioral and ecologic effects of differential predation pressure on moose in Alaska. *Journal of Mammalogy* 82:422-429.
- WILLIAMS, C. K., R. S. LUTZ, and R. D. APPLGATE. 2003. Optimal group size and northern bobwhite coveys. *Animal Behaviour* 66:377-387.
- ZAITSEV, V. A. 1983. Escape behaviour of musk deer (*Moschus moschiferus parviceps*) in middle Sikhote-Alin. *Zoologicheskyy Zhurnal* 62:1718-1726.