

## Life cycle period and activity of prey influence their susceptibility to predators

A. Molinari-Jobin, P. Molinari, A. Loison, J.-M. Gaillard and U. Breitenmoser

Molinari-Jobin, A., Molinari, P., Loison, A., Gaillard, J.-M. and Breitenmoser, U. 2004. Life cycle period and activity of prey influence their susceptibility to predators. – *Ecography* 27: 323–329.

In a multi-prey system, predators kill different kinds of prey according to their availability, where “availability” is a function of prey abundance and vulnerability (e.g. anti-predator behavior). We hypothesized that prey availability changes seasonally, for instance because reproduction leads to a higher abundance of young in spring and summer or because changes in behavior such as during the mating season makes the prey periodically more vulnerable. We tested this hypothesis in a simple predator-prey system in the Jura Mountains of Switzerland and France, where a single large mammalian predator, the Eurasian lynx, preys upon two ungulate species, the roe deer and the chamois. In 1996 and 1997 we were able to assign a total of 190 roe deer and 54 chamois killed by lynx to a specific age and sex class (males, females or juveniles). As expected, the proportion of juveniles killed varied considerably among periods, being at the highest from 1st of June to 15th of August. No significant seasonal differences were detected regarding the frequency of predation on males versus females. In particular, the interaction between species and period, expected because of different timing of the rutting period between roe deer and chamois, was not significant. Females were killed only slightly more often during gestation. The relationship between prey abundance and vulnerability is highly complex, as the lynx’ prey selection needs to be analyzed not only horizontally (changes of a specific prey category with season) but also vertically (an increase in the vulnerability of one category releases predation pressure on others). Second, we predicted that certain activities, such as feeding, expose prey to predation more than others. We found more chamois predated when feeding, whereas roe deer were predated mainly when ruminating. This interspecific discrepancy reflects differences either in the anti-predator behavior of roe deer and chamois or in the relative time allocation to feeding and ruminating between the two species.

*A. Molinari-Jobin (jobinmolinari@aol.com), Swiss Lynx Project, Rüti 62C, CH-3855 Schwanden, Switzerland. – P. Molinari, Univ. of Padova, Via A. Diaz 90, I-33018 Tarvisio, Italy. – A. Loison and J.-M. Gaillard, UMR CNRS 5558, Univ. Claude Bernard Lyon 1, F-69622 Villeurbanne Cedex, France. – U. Breitenmoser, Inst of Veterinary Virology, Univ. of Bern, Länggassstrasse 122, CH-3012 Bern, Switzerland.*

The mere presence of predators – or even only the threat of predation – may influence prey behavior (for a review see Lima and Dill 1990). However, evidence of the effect of anti-predator behavior on mortality patterns in natural systems is rare (Sinclair and Arcese 1995). It is generally believed that felids, which rely on surprise attacks when hunting, kill a random sample of prey

individuals (Caro and FitzGibbon 1992). An essential quality of a felid’s hunting method is that the predator remains undetected by the quarry. Once discovered, the cat abandons the hunt (Kruuk 1986). The renouncement of pursuit has important consequences for prey individuals: they can avoid predation by maintaining a high vigilance level. However, prey animals have conflicting

Accepted 26 January 2004

Copyright © ECOGRAPHY 2004  
ISSN 0906-7590

demands between being vigilant, thus avoiding predation, and other activities. Depending on their immediate needs, they will have to vary the sensitivity of their behavior to predation risk, and consequently be more or less vulnerable.

Since an animal must accomplish more in its lifetime than simply avoid predation, there might be times when it has to run a greater risk of predation than usual. Yet few failures are as unforgiving as the one to avoid a predator. Certain characteristics of prey may make them more vulnerable to predation, but what are those? To identify ecological and behavioural traits of prey that are correlated with predation risk it is necessary to improve our understanding of predation as a selective force.

In a multi-prey system, predators kill different kinds of prey according to their availability, where "availability" is a function of prey abundance and anti-predator behavior (vulnerability). The predators prey selection should track changes in prey availability. Those changes may be due to alterations in abundance, for instance seasonally through reproduction or migration, but also through temporal or periodical changes in behavior that makes the prey more vulnerable, for instance during the mating season (Caro and FitzGibbon 1992).

In the Jura Mountains of Switzerland and France, the Eurasian lynx *Lynx lynx* preys upon two ungulate species, the roe deer *Capreolus capreolus* and the chamois *Rupicapra rupicapra*. These two ruminants make up 90% of the lynx' preys in the Jura Mountains, alternative preys being of no quantitative importance (Jobin et al. 2000). Such a quite simple predator prey system offers a unique opportunity to test how the life cycle period and activity of the prey influence their susceptibility to predation. Despite considerable knowledge of the food habits of lynx (Okarma et al. 1997, Jobin et al. 2000), differential predation risk according to the life cycle period and stages of the prey has never been assessed. We tried to fill this gap by intensively monitoring radio-collared lynx during all seasons for two consecutive years.

Roe deer and chamois are highly sedentary (roe deer: Strandgaard 1972, Thor 1995 for an example in mountains, chamois: Loison et al. 1999) and live on small home ranges (about 30–200 ha, Andersen et al. 1998, Hardenberg et al. 2000) compared to lynx (about 16 800–26 400 ha, Breitenmoser et al. 1993). Therefore, we can assume that the pool of prey available to the lynx is approximately constant within the year, the only difference consisting in the seasonally higher availability of young in spring (Andersen et al. 1998, Loison 1995). We tested the three following predictions (Table 1): 1) a higher proportion of juveniles among preys recovered during summer because of both the higher availability (see above) and higher susceptibility of this age-class (Linnell et al. 1995); 2) a higher proportion of males among preys recovered during the rutting period

Table 1. Summary of predictions concerning hypotheses that 1) the predation pattern of lynx is seasonal and 2) the activity patterns of both roe deer and chamois influence their vulnerability to lynx predation.

Prediction	Outcome
1.1. A higher proportion of juveniles among prey killed during lactation and roe deer rut.	Supported
1.2. A higher proportion of males among prey killed during the species-specific rutting periods.	Rejected for chamois and partly supported for roe deer
1.3. A higher proportion of females among prey killed during gestation and lactation.	Rejected
2. Activity patterns just before death different between chamois and roe deer.	Supported

(summer for roe deer, autumn for chamois) due to more conspicuous behavior of males (roe deer: Johansson et al. 1995; chamois: Lovari and Locati 1991); and 3) a higher proportion of females among preys recovered during gestation and lactation due to higher energetic needs, that may force them to adopt more risky tactics while feeding.

Second, we tested whether the activity patterns just before death were the same in the two prey species (Table 1). Two explanations could lead to reject similar predation risks according to the activity in roe deer and chamois. 1) A behavioral explanation, by which the predation risk is expected to be similar when roe deer are foraging and ruminating, as they are secretive and use the same area for both activities, while predation risk should be higher when foraging than ruminating in chamois, because they use remote area only for ruminating. This is reflected in the between-species difference in home range size for a similar body mass (< 50 ha for roe deer in a mountain habitat, Thor 1995; up to 200 ha for chamois in mixed habitat, Hardenberg et al. 2000) 2) A life history explanation, by which roe deer and chamois have different eating habits (mixed feeder tactic for chamois, browser for roe deer, Hofmann 1989) that is associated with different overall activity patterns, roe deer being active about 50% of the time, while chamois may be active up to 75% of the time (Mysterud 1998). Even in the absence of difference of predation risk according to the activity, this difference in time budget between roe deer and chamois could lead lynx to have highest chance to prey on chamois when foraging.

## Study area

The study was conducted in the Jura Mountains, a secondary chain of limestone mountains forming the north-western border of Switzerland with France.

The altitude ranges from 372 (Lake Geneva) to 1679 m a.s.l. (summit of Mont Tendre). Over 60% of the study area lies above 1000 m a.s.l. Mean monthly temperatures ranged from  $-6^{\circ}$  in January to  $15^{\circ}\text{C}$  in July. Snow depth during winter varied from 0 to over 100 cm depending on elevation, exposure and year. The main study area was confined to the northern part (Jura Mountains) of the canton of Vaud (VD) covering 710 km<sup>2</sup>. Lynx were also followed in the adjoining areas of the canton of Neuchâtel (NE) and in France, the total area being ca 3000 km<sup>2</sup>. Deciduous forests along the slopes and coniferous forests on the ridges cover 53% of the highlands. The forest is commercially managed through shelter-wood cutting. These mixed forests, with the main tree species beech *Fagus sylvatica*, spruce *Picea abies* and white spruce *Abies alba*, and the adjoining open areas offer high quality habitat for ungulates. The ungulate community consists of red deer *Cervus elaphus*, roe deer, chamois and wild boar *Sus scrofa*. In 1996 and 1997, 698 and 1033 roe deer and 79 and 78 chamois were hunted annually. Both in roe deer and chamois, males and females were hunted in equal proportions. Roe deer were hunted during 18 days a year in autumn and chamois during 8 days in early winter. Wild ungulates are not fed during winter. During summer the open areas are used as pastures for cattle. Sheep are rare in the Swiss part of the Jura Mountains. Lynx were the only large predator in the study area. Wolves *Canis lupus* and brown bears *Ursus arctos* were exterminated in the 18th and 19th centuries (Breitenmoser 1998).

## Methods

Between April 1988 and June 1998, a total of 29 different lynx were live-trapped and radio-collared following procedures described in Jobin et al. (2000). Radio-collared lynx were subsequently relocated from the ground. Locations were assigned to one of three accuracy levels (1 km<sup>2</sup>, 1 ha, or direct observation) depending on bearing distance, activity of lynx, and additional observation. From January 1996 through December 1997, special efforts were made to find kills. We therefore monitored the movements of individual lynx daily. Lynx usually fed for several days on a kill, hiding during the day and returning to the carcass each evening. If lynx stayed for more than half an hour in one place at dusk, we located it precisely by approaching it to a distance of about 50–200 m. The next day this area was scanned with a Bavarian bloodhound. With the aid of the dog, we could be sure also to find kills that are consumed in less than two days, i.e. red foxes *Vulpes vulpes*, brown hares *Lepus europaeus*, and roe deer fawns and chamois kids during their first two months of life. For each kill, the species was recorded. Whenever possible, the heads of the kills were collected to

determine the age and sex of the animal. Chamois and roe deer were defined as juveniles from birth to the end of May of the following year. We did not take account of the sex of juveniles thus pooling them into a single age category.

In 1996 and 1997, the main study area was occupied by 3 male, 5 female and 3 subadult lynx (Swiss Lynx Project, unpubl.). Since there are clear differences in the prey preference of lynx age and sex classes (Molinari-Jobin et al. 2002), we searched for kills of male, female and subadult lynx according to their occurrence in the population.

We divided the year into six periods reflecting the life cycle of the two species: gestation from 1 April to 30 May; lactation from 1 June to 15 July; roe deer rut from 16 July to 15 August; autumn from 16 August to 31 October; chamois rut from 1 November to 31 December; winter from 1 January to 31 March. For roe deer, the definition of the rutting period was restricted to the rutting period of females (Andersen et al. 1998). To test the influence of these periods on the proportion of roe deer, males and juveniles among the recovered animals, we fitted generalized linear models using the relevant variables among the following 4 factors: life cycle periods, species, age and sex. And because the sampling occurred over 2 yr, we checked the consistency of the results over years.

It is usually not possible to get direct evidence of an effect of the activity on the prey vulnerability as it is extremely difficult to directly observe predation in forest habitat. To assess the activity of an ungulate prey just before death, we checked the mouth of each ungulate kill for contents. We distinguished between three activities: 1) the ungulate was feeding, when we found solid leaves in the mouth, 2) the ungulate was ruminating, when the mouth contained regurgitated material, and 3) other activities, when the mouth was empty. We focused on the feeding and ruminating activities. Using generalized linear models, we then tested the effect of species, sex and age, taking into account the effects of year and period of life cycle on the proportion of recovered animals feeding or ruminating. All the statistical analyses were performed using Splus (Venables and Ripley 1994).

## Results

### Overall analysis

In 1996 and 1997 we assigned a total of 190 roe deer and 54 chamois to a specific age and sex class. The overall proportion of roe deer among the prey recovered was 77.8%. The two-way interactions between year and period ( $\chi^2 = 7.816$ , DF = 5,  $p = 0.167$ ) and between the age-sex category and period ( $\chi^2 = 6.894$ , DF = 10,  $p = 0.735$ ) were not significant, while the interaction

between the age-sex category and year was close to significance ( $\chi^2 = 5.859$ ,  $DF = 2$ ,  $p = 0.053$ ). This last interaction was actually due to a difference between years in the proportion of roe deer vs chamois females recovered (year effect when the analysis is performed on the adult females only:  $\chi^2 = 4.222$ ,  $DF = 1$ ,  $p = 0.040$ ; on the adult males only:  $\chi^2 = 0.018$ ,  $DF = 1$ ,  $p = 0.894$ ; on the juveniles only:  $\chi^2 = 0.836$ ,  $DF = 1$ ,  $p = 0.361$ ). There was indeed a larger proportion of female roe deer recovered in 1997 (91.1%) than in 1996 (73.2%, Fig. 1). The main effect of period was not significant ( $\chi^2 = 3.200$ ,  $DF = 5$ ,  $p = 0.669$ ).

### Proportion of juveniles

We did not detect any two-way interactions among species, year and period on the proportion of juveniles (all  $p > 0.08$ ). There were no differences between years ( $\chi^2 = 0.133$ ,  $DF = 1$ ,  $p = 0.716$ ) or between species ( $\chi^2 = 0.174$ ,  $DF = 1$ ,  $p = 0.676$ ). But as expected in prediction 1.1 (Table 1), the proportion of juveniles varied a lot among periods ( $\chi^2 = 15.817$ ,  $DF = 5$ ,  $p = 0.007$ ) being at the highest during periods 2 and 3 (from 1 to 15 August) and at the lowest during period 1 (from 1 April to 30 May, Fig. 2). These periods correspond respectively to the whole lactation stage when many small offspring are available to lynx (periods 2 and 3) and to the gestation stage (period 1) when 10–11 months-old juveniles have reached  $> 60\%$  of their adult body size (roe deer: Gaillard et al. 1993; chamois: Loison 1995).

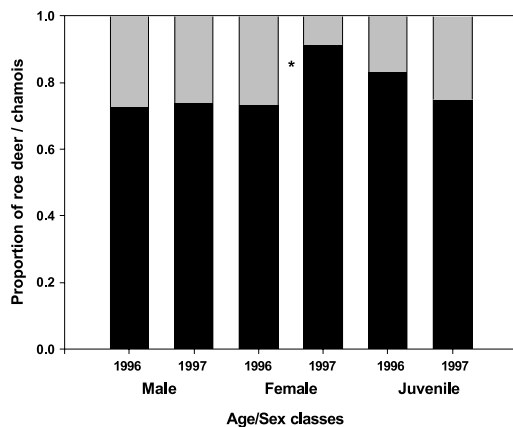


Fig. 1. Comparison of roe deer (black,  $n = 190$ ) and chamois (grey,  $n = 54$ ) age/sex classes killed between the two years. The only significant difference is marked with an asterisk.

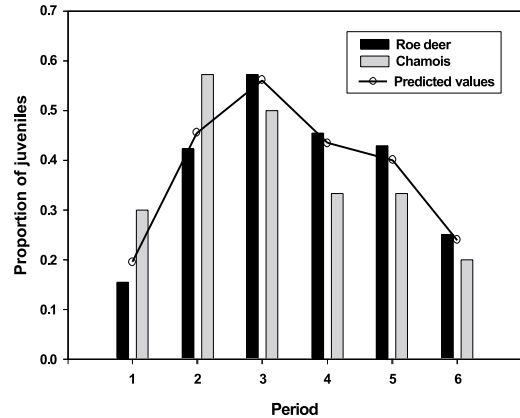


Fig. 2. Seasonal differences in roe deer fawns and chamois kids killed. The total number of roe deer and chamois killed per period equals: 1 = gestation: 26 roe deer and 10 chamois; 2 = lactation: 26 roe deer and 7 chamois; 3 = roe deer rut: 21 roe deer and 4 chamois; 4 = autumn: 44 roe deer and 9 chamois; 5 = chamois rut: 21 roe deer and 9 chamois; 6 = winter: 52 roe deer and 15 chamois.

### Proportion of males

The overall proportion of males was 51.0% among recovered animals. There were no significant two-way interactions among year, species and period on the proportion of males (all  $p > 0.39$ ). In particular, contrary to the predictions 1.2 and 1.3 (Table 1), the interaction between species and period was not significant ( $\chi^2 = 4.224$ ,  $DF = 5$ ,  $p = 0.518$ ). Main effects of period ( $\chi^2 = 4.003$ ,  $DF = 5$ ,  $p = 0.549$ ) and species ( $\chi^2 = 1.774$ ,  $DF = 1$ ,  $p = 0.183$ ) were not significant either, although in chamois more males were killed than in roe deer. Only between-year differences occurred in the proportion of males recovered ( $\chi^2 = 4.184$ ,  $DF = 1$ ,  $p = 0.041$ ). The proportion of males was 15.2% higher in 1997 than in 1996.

### Activity of prey

The activity of prey was assessed for a total of 143 roe deer and 44 chamois. We first analyzed the proportion of prey found ruminating vs other activities. The 2-way interactions between species and period, species and the age-sex category and period and the age-sex category were non significant (all  $p > 0.27$ ). The main effect of the period was not significant ( $\chi^2 = 9.511$ ,  $DF = 5$ ,  $p = 0.090$ ; in period 3 the quarry was most often killed when ruminating) while both the main effect of the age-sex category ( $\chi^2 = 8.578$ ,  $DF = 2$ ,  $p = 0.014$ ; females were more often killed when ruminating than males or juveniles) and of the species ( $\chi^2 = 28.275$ ,  $DF = 1$ ,  $p < 0.001$ ) were significant. No chamois males, no

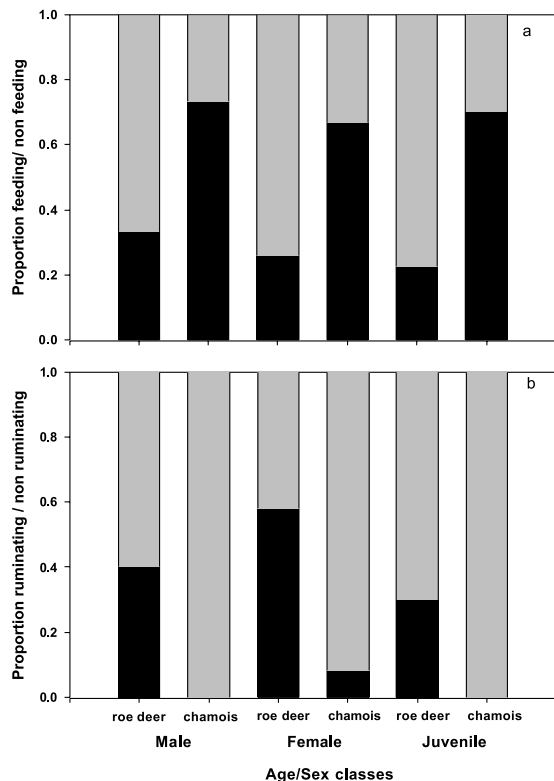


Fig. 3. Comparison between the activity that rendered the different roe deer and chamois age/sex classes vulnerable to lynx predation. (a) Feeding ( $n$  roe deer = 34,  $n$  chamois = 26). (b) Ruminating ( $n$  roe deer = 59,  $n$  chamois = 1).

chamois juveniles and only one chamois female (8.0%) were ruminating while killed. In contrast, the proportion of roe deer ruminating when killed was much larger: 40.0% of males, 58.0% of females and 30.0% of juveniles (Fig. 3). No additional effect of year was found ( $\chi^2 = 0.050$ ,  $DF = 1$ ,  $p = 0.823$ ).

We then repeated the analyses using the proportion of prey recovered found eating. None of the 2-way interactions between species, period and the age-sex category were significant (all  $p > 0.10$ ). Among the main effects, only species was significant ( $\chi^2 = 22.393$ ,  $DF = 1$ ,  $p < 0.001$ ). The proportion of chamois preys found eating was 70.3% while only 27.4% of roe deer preys were killed when eating (Fig. 3). The main effects of period ( $\chi^2 = 1.286$ ,  $DF = 5$ ,  $p = 0.936$ ) and the age-sex category ( $\chi^2 = 1.301$ ,  $DF = 2$ ,  $p = 0.522$ ) were both not significant.

## Discussion

The analysis of the prey selection of lynx in the Jura Mountains revealed that not only the abundance of the different prey categories, but also periodical changes in

behavior and activity had an influence on prey availability. The interactions of prey abundance and vulnerability are highly complex, as the lynx' prey selection needs to be analyzed not only horizontally (changes of a specific prey category with season) but also vertically (an increase in the vulnerability of one category releases predation pressure on the others).

We searched for intraspecific age and sex differences in the frequencies among prey killed. Lynx are stalking predators, and most chases are short. In such ambush situations there may be little room for selection. Thus, lynx predation has been shown to be uniform across roe deer populations (Aanes et al. 1998). However, the seasonal analysis of the predation revealed that lynx did not kill the different age and sex classes only according to abundance. Rather, the prey selection followed a seasonal pattern. The most obvious finding was that roe deer does were not the prey category most frequently killed. Instead, roe deer fawns were clearly most often killed from 1 June to 31 October. Lynx clearly responded to the higher availability of juveniles during summer. An analysis of the changes in the seasonal frequency of roe deer fawns among kills showed great seasonal fluctuations, thus confirming prediction 1.1 (Table 1). In contrast, prediction 1.2 was not confirmed because roe deer bucks were not most often killed during the rut, although the number of male roe killed increased during the rut compared to the periods immediately before or after (Fig. 4). However, these two predictions should not be interpreted separately. Indeed, roe deer bucks may have been released from predation pressure by the high availability of juveniles during this critical period. Prediction 1.3 had to be rejected, too (Table 1). While roe deer does were killed most often during gestation, we were unable to detect changes in the female frequency among preys during the lactation period (Fig. 4). Again, the high availability of juveniles may provide a relative protection for their mothers. In chamois, females and fawns were – in contrast to our prediction – killed with the same frequency during the rut as males (Fig. 4).

As expected, the activity patterns just before death differed between roe deer and chamois. A striking result was the quasi absence (only 1 female) of chamois preyed upon when ruminating. By retreating into steep, rocky areas where it is difficult for lynx to hunt and where they can spot an approaching predator early, chamois are highly secure when ruminating. On the contrary, the largest proportion of roe deer were preyed upon when ruminating. Adult roe deer prefer to bed down below dense canopy (Mysterud 1996). Even though this may lower the probability of the predator discovering the bedded deer, it may on the other hand allow lynx to approach undetected. Roe deer rely more on their hearing and smell than on sight (Raesfeld 1985). But when ruminating, the sense of hearing may be greatly

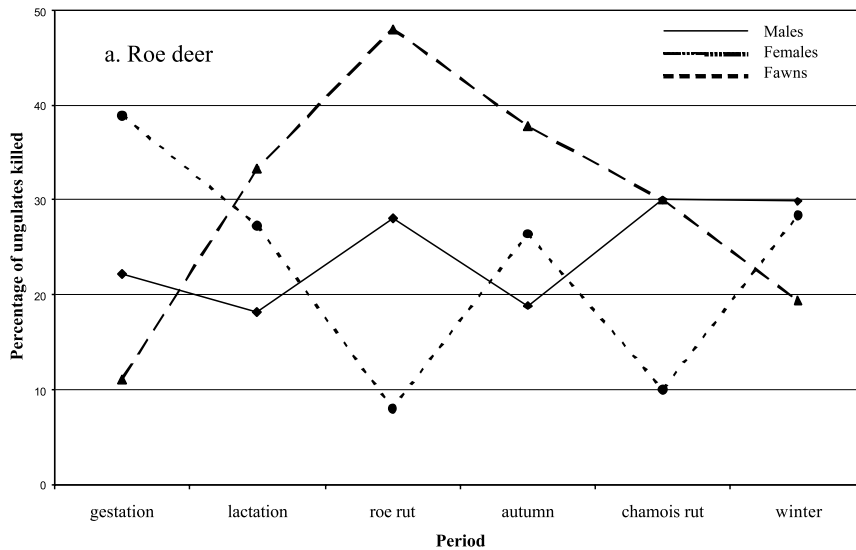
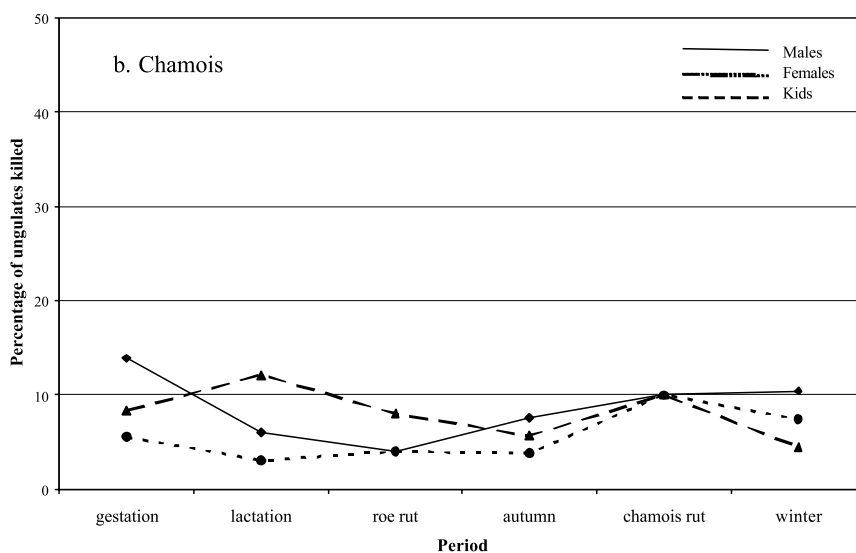


Fig. 4. Seasonal pattern of the percentage of (a) roe deer and (b) chamois killed by lynx from 1996–1997 (gestation,  $n = 36$ ; lactation,  $n = 33$ ; roe rut,  $n = 25$ ; autumn,  $n = 53$ ; chamois rut,  $n = 30$ ; winter,  $n = 67$ ). Percentage were calculated on the total number of preys per period irrespective of the species.



hindered. Such difference between species might provide support for the behavioral explanation, and cannot be only accounted for by different time budget.

The susceptibility to lynx depends not only on the activity, but also on the relative vulnerability of other prey classes. From the observed pattern of predation we concluded that each season, one sex/age class of a prey species stands out in its vulnerability to lynx. The relative predation risk of one category depends on the predation risk of the others. Lynx killed prey successfully when the anti-predator behavior of the prey was insufficient, as they had to compromise with other activities, such as feeding and social interactions. In this passive choice, predator preferences are the result of traits of the prey and not predator selectivity (Pastorok 1981). Each season, individuals of a certain prey

category may relax their anti-predator behavior in favor of other activities. We described behaviors where prey individuals were vulnerable. However, the same individual is not vulnerable to lynx predation all the time. We do not know how prey animals assess the immediate potential risk of predation and what they do to avoid predation. In future work, it would be important to compare the behavior of roe deer and chamois in areas where predation risk is high, low and non-existent to assess what prey animals do to successfully avoid predation as well as the impact of predator-avoidance-behavior on population dynamics.

*Acknowledgements* – We thank J. Auer, Ch. Breitenmoser-Würsten, S. Capt, M. Conti, P. Deleury, D. Gétaz, J.D. Horn, A. Kessler and R. Kessler, S. Knispel, P. Matthieu, R. Pensa, J. Renaud, B. Reymond, G. Rizzi, D. Rosilici, S. Roy, J. C. Sarria,

S. Schadt, M. Scholl, D. Schwarz, P. Wandeler, and F. Zimmermann for assistance with field work. We would also like to thank M. Scholl for piloting the search flights. We thank P. Kjellander, A. Mysterud and W. Nentwig for comments on earlier drafts and A. and P. Jackson for improving the English. The study was funded by the Swiss Agency for Environment, Forest and Landscape (SAEFL), the canton of Vaud, the Swiss League for Protection of Nature (Pro Natura) and WWF Switzerland.

## References

- Aanes, R. et al. 1998. Roe deer as prey. – In: Andersen, R., Duncan, P. and Linnell, J. D. C. (eds), *The European roe deer: the biology of success*. Scandinavian Univ. Press, pp. 139–159.
- Andersen, R. et al. 1998. *The European roe deer: the biology of success*. – Scandinavian Univ. Press.
- Breitenmoser, U. 1998. Large predators in the Alps: the fall and rise of man's competitors. – *Biol. Conserv.* 83: 279–289.
- Breitenmoser, U. et al. 1993. Spatial organization and recruitment of lynx (*Lynx lynx*) in a re-introduced population in the Swiss Jura Mountains. – *J. Zool.* 231: 449–464.
- Caro, T. M. and FitzGibbon, C. D. 1992. Large carnivores and their prey: the quick and the dead. – In: Crawley, M. J. (ed.), *Natural enemies*. Blackwell, pp. 117–142.
- Gaillard, J. M. et al. 1993. Roe deer survival patterns: a comparative analysis of contrasting populations. – *J. Anim. Ecol.* 62: 778–791.
- Hardenberg, A. et al. 2000. Male alpine chamois occupy territories at hotspots before the mating season. – *Ethology* 106: 617–630.
- Hofmann, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. – *Oecologia* 78: 449–457.
- Jobin, A., Molinari, P. and Breitenmoser, U. 2000. Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains. – *Acta Theriol.* 45: 243–252.
- Johansson, A., Liberg, O. and Wahlström, L. K. 1995. Temporal and physical characteristics of scraping and rubbing in roe deer (*Capreolus capreolus*). – *J. Mammal.* 76: 123–129.
- Kruuk, H. 1986. Interactions between felidae and their prey species: a review. – In: Miller, S. D. and Everett, D. D. (eds), *Cats of the world: biology, conservation, and management*. Kingsville, pp. 353–374.
- Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. – *Can. J. Zool.* 68: 619–640.
- Linnell, J. D. C., Aanes, R. and Andersen, R. 1995. Who killed bambi? The role of predation in the neonatal mortality of temperate ungulates. – *Wildlife Biol.* 1: 209–223.
- Loison, A. 1995. *Approches intra- et inter-spécifiques de la dynamique des populations: l'exemple du chamois*. – Ph.D. thesis, Univ. of Lyon.
- Loison, A., Jullien, J. M. and Menaut, P. 1999. Subpopulation structure and dispersal in two populations of chamois. – *J. Mammal.* 80: 620–632.
- Lovari, S. and Locati, M. 1991. Temporal relationships, transitions and structure of the behavioural repertoire in male apennine chamois during the rut. – *Behaviour* 119: 77–103.
- Molinari-Jobin, A. et al. 2002. Significance of lynx *Lynx lynx* predation for roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra* mortality in the Swiss Jura Mountains. – *Wildlife Biol.* 8: 109–115.
- Mysterud, A. 1996. Bed site selection by adult roe deer *Capreolus capreolus* in southern Norway during summer. – *Wildlife Biol.* 2: 101–106.
- Mysterud, A. 1998. The relative roles of body size and feeding type on activity time of temperate ruminants. – *Oecologia* 113: 442–446.
- Okarma, H. et al. 1997. Predation of Eurasian lynx on roe deer and red deer in Bialowieza Primeval Forest, Poland. – *Acta Theriol.* 42: 203–224.
- Pastorok, R. A. 1981. Prey vulnerability and size selection by *Chaoborus* larvae. – *Ecology* 62: 1311–1324.
- Raesfeld, F. 1985. *Das Rehwild*. – Paul Parey.
- Sinclair, A. R. E. and Arcese, P. 1995. Population consequences of predation-sensitive foraging: the Serengeti wildebeest. – *Ecology* 76: 882–891.
- Strandgaard, H. 1972. The roe deer (*Capreolus capreolus*) population at Kalo and the factors regulating its size. – *Danish Rev. Game Biol.* 7: 1–205.
- Thor, G. 1995. Ecology of a free-ranging roe deer population in the Swabian mountains and impact of management measures. – *Proc. Second European Roe Deer Meeting*. Munich Wildlife Society, Munich.
- Venables, W. and Ripley, N. 1994. *Modern applied statistics with S-PLUS*. – Springer.