HOLARCTIC ECOLOGY 7: 300–304. Copenhagen 1984

Predation on brown hare and ring-necked pheasant populations in southern Sweden

Sam Erlinge, Bo Frylestam, Görgen Göransson, Göran Högstedt, Olof Liberg, Jon Loman, Ingvar N. Nilsson, Torbjörn von Schantz and Magnus Sylvén

Erlinge, S., Frylestam, B., Göransson, G., Högstedt, G., Liberg, O., Loman, J., Nilsson, I. N., Schantz, T. von and Sylvén, M. 1984. Predation on brown hare and ring-necked pheasant populations in southern Sweden. – Holarct. Ecol. 7: 300–304.

Predation on brown hares and pheasants in relation to their production was examined in an open field area in southern Sweden. Biomass and numbers of hares and pheasants eaten by the predators were calculated from data on food habits, food requirements, and numbers of the mammalian and avian predators present (11 species). At the same time estimates of numbers and production of hares and pheasants were obtained. At least 40% of the estimated annual production of hares and almost 60% of subadult-adult pheasants in autumn were consumed by the predators. Estimated numbers of hares and pheasants taken by the predators greatly exceeded shooting and road mortality. Foxes and cats were the predominant predators on hares (about 90% of total hare consumption). Foxes accounted for about two-thirds of predation on pheasants; cats and goshawks were of secondary importance. Pheasant nests were preyed upon by hooded crows and also by badgers. Hares and pheasants contributed only about 3 and 1%, respectively, of the food of the predators.

S. Erlinge, B. Frylestam, G. Göransson, G. Högstedt, O. Liberg, J. Loman, I. N. Nilsson, T. von Schantz and M. Sylvén, Dept of Animal Ecology, Univ. of Lund, Ecology Building, S-223 62 Lund, Sweden.

1. Introduction

The influence of predation on dynamics of vertebrate prey populations is poorly known and general opinions greatly diverge (for reviews see e.g. Errington 1946, Keith 1974). The question is even more controversial concerning game populations, as predators may reduce the hunting bag and act as competitors with hunters.

In this paper we estimate consumption of brown hares *Lepus europaeus* Pallas and ring-necked pheasants *Phasianus colchicus* L. by predators in relation to the production of these two prey species. We also examine the impact of predation as compared to shooting and road mortality.

2. Study area and populations of predators and prey

The study was performed in an open field area (the Revinge area) in southern Sweden. The area of about 40 km^2 is used for military training and cattle grazing. Grazed fields and sandy hills with copses of coniferous trees represent the dominant habitat with smaller areas (about 500 ha) consisting of wet meadows and marshes. The preferred habitat of hares was grazed fields, whereas pheasants preferred wet meadows (for details see Frylestam 1979 and Göransson 1980). Rabbits *Oryctolagus cuniculus* L. inhabiting the drier areas were the predominant prey of the predators. Field voles *Microtus agrestis* L. and water voles *Arvicola terrestris* L., other important prey, occurred mainly in wet meadows.

Several mammalian and avian predators occurred in the area. The following predator species were included in the study: red fox *Vulpes vulpes* L., domestic cat *Felis catus* L., badger *Meles meles* L., polecat *Mustela putorius* L., stoat *Mustela erminea* L., common buzzard *Buteo buteo* L., European kestrel *Falco tinnunculus* L.,

Accepted 3 June 1983

goshawk *Accipiter gentilis* L., tawny owl *Strix aluco* L., long-eared owl *Asio otus* L. and hooded crow *Corvus cornix* L.

3. Methods and material

3.1. Estimating densities and productivity of hares

Estimates of population density were obtained by counting hares in sample plots during nights in spring and autumn (Frylestam 1981). The number of hares born annually was estimated on the basis of the number of reproductive females and the mean number of young per female (Frylestam 1980).

3.2. Estimating densities and productivity of pheasants

The breeding population density of pheasants was estimated by counting territorial cocks and considering the sex ratio (Göransson 1980). Crowing cocks were located and mapped in April and May according to Kimball (1949) and Burger (1966). The sex ratio was determined by counting cocks and hens in mornings and evenings when pheasants were foraging in open areas. The estimates of the autumn population were based on spring numbers, summer mortality of hens and recruitment (Dale 1952, Wagner et al. 1965). Summer mortality was calculated from data on radio-tracked hens (Göransson 1980) and recruitment according to Dale (1952) from age and sex ratio of trapped and shot pheasants.

3.3. Estimating hare and pheasant consumption by the predators

The biomass and numbers of hares and pheasants eaten by the predators were calculated from data on food habits, total food requirements, and predator numbers. Information on food habits was obtained by analyses of pellets of raptors and owls, and of scats and prey remnants of carnivores. Correction factors for multiplying weights of food remains to calculate figures on ingested fresh biomass were obtained from feeding experiments (details are given in papers dealing with the separate predators: von Schantz 1980, Erlinge 1981, Nilsson 1981, Liberg 1982 and also Erlinge et al. 1983). Food requirements of the predators at different seasons were obtained from cage experiments and from literature reports (see the above references). The predator populations were censused at different seasons of the year with emphasis on the periods before and after the breeding season (Liberg 1981, Nilsson 1981, von Schantz 1981, Sylvén 1982, Erlinge 1983, Erlinge et al. 1983).

3.4. Problems of identifying hare and pheasant remains in scats

Separation of hares and rabbits in the scats was difficult because hairs of the two species have similar characteristics (Brunner and Coman 1974). Careful examination of a reference hair collection of the two species showed that two features were useful for species identification, i.e., the shape and appearance of cross-sections near the base of hairs and the scale pattern in the shield region of hairs (see also Brunner and Coman 1974). The accuracy of these criteria was tested on known hair samples from rabbits and hares. Correct identification was made in 45 out of 50 cases and in the remaining five cases separation was not possible.

In the field samples lagomorph remains were found in 2189 cases (Tab. 1). In 871 of these (40%) hare/rabbit separation was possible.

Tab. 1. Sample sizes (scats, pellets, and prey remnants) for the predators examined.

Predator			Lagomorph occurrence (%)	No. of cases where separation between hare and rabbit was possible	No. of cases with identified hare remains
Vulpes vulpes	1190	scats and prey remnants at dens	86	295	24
Felis catus	1552	scats and prey remnants	32	257	22
Meles meles	657	scats	15	32	1
Mustela putorius	512	scats	33	72	4
Mustela erminea	1006	scats	4	25	1
Buteo buteo	1519	pellets and prey remnants in nests	19	165	4
Strix aluco	1636	prey items[1]	2	25	4
Asio otus	7811	prey items[1]	0.1	0	0
Falco tinnunculus	746	prey items[1]	0	0	0

[1]Total number of occurrences in the pellet sample.

Avian prey were identified by feather analyses (Day 1966). Pheasants were the only galliform species in the area which allowed ready identification. Analysis of predation on pheasants had to be restricted to subadults and adults because feeding tests with carnivores showed that chick feathers were completely digested.

4. Results and discussion

4.1. Relative importance of hare and pheasant as food for predators

On an annual basis hares and pheasants contributed little to the predators' diet, i.e., about 3 and 1% respectively of the estimated total prey consumption (Tab. 2). For the foxes, however, pheasants were a somewhat more important prey during the denning period (May and June), making up about 5% of their diet (von Schantz 1980).

There are no corresponding data from other agricultural areas where predation on both hares and pheasants has been considered as well as the whole predator guild. In an agricultural area in Wisconsin pheasants were unimportant for the red fox (2–3% of its diet) (Pils and Martin 1978), whereas in a Polish study brown hares made up 26% of the foxes diet (Goszczynski et al. 1976). In the latter area other predators were investigated (marten, *Martes martes,* badger, cat, buzzard and owl) and in each predator's diet hare contributed less than 5%. Hares also were important for foxes in another Polish area, making up 46% of the foxes' annual food (Pielowski 1976a). In our area as well as in that in North America, where field game was unimportant for the predators, rabbits were abundant and made up the major part of the predators' food. In Poland on the other hand where hares were important for foxes, there were no rabbits. In a forested area in Canada, hares were of great importance for several predators (Keith et al. 1977). This case, however, concerned the cyclic snowshoe hare *Lepus americanus* with extremely high densities during peak years, a situation very different from ours.

4.2. Predation in relation to other mortality factors

The estimated number of hares taken by the predators greatly exceeded that from hunting by man (Tab. 3). The figure on predator-eaten hares is probably an underestimate as predation by hooded crows was not included; crow predation on young hares was observed, but data were too few to allow calculations. In pheasants (subadults and adults) the estimated number consumed by the predators was more than twice that due to hunting and four times that due to road mortality (Tab. 3). However, all prey eaten by predators are not necessarily killed by them. That problem is discussed below.

4.3. Relative importance of the predatory species

Foxes and cats were the predominant predators on hares accounting for about 90% of total hare consumption, both in terms of biomass and numbers (Tab. 4). Polecat, common buzzard, and tawny owl were less important, whereas stoat, badger, and long-eared owl fed on hares only occasionally, and no record was obtained for kestrel.

The average size of hares taken by cats was smaller than that taken by foxes (von Schantz 1980, Liberg 1981). Thus, in terms of numbers, predation by cats exceeded that of foxes, although the biomass of hares eaten by foxes was larger (Tab. 4).

Foxes accounted for about two-thirds of the preda-

Tab. 2. Estimates of the annual consumption of different prey by predators; means of 1975 and 1976. Other prey mainly consisted of earthworms and amphibians.

	Hare	Pheasant	Rabbit	Small rodents	Other prey	Total
Amount (kg)	898	272	16867	6719	9592	34348
Per cent	2.6	0.8	49.1	19.3	28.2	100

Tab. 3. Annual predation and other mortality in relation to production (means of 1975 and 1976) of pheasants (hatched chicks) and hares. As the hare and pheasant populations remained stable in these years we assume that total annual losses equal production.

	Annual production	Annual losses	Estimated min. number consumed by predators	Losses due to hunting	Losses due to traffic
Number of:					
hares	1970	≤1970	746 (38%)	118 (6%)	?
pheasants ≤12 weeks		625	362 (58%)	144 (23%)	75 (12%)

Tab. 4. Estimated annual consumption of hares and pheasants by different predator species; mean values of 1975 and 1976.

	Vulpes vulpes	*Felis catus*	*Accipiter gentilis*	Other predators	Total
Hare					
Biomass (kg)	579	230	–	88	897
Per cent	64	26		10	100
Number	260	369	–	117	746
Per cent	35	49		16	100
Pheasant (≥12 weeks)					
Number[1]	232	54	58	18	362
Per cent	64	15	16	5	100

[1]Mean body weight is 1.0 kg.

Tab. 5. Predation on pheasant nests during egg-laying and incubation periods: n is the number of nests preyed upon.

	Predator			Total
	Corvus cornix	*Meles meles*	Unknown	losses
Egg-predation (%) during:				
laying (n=147)	70	10	–	80
incubation (n=36) .	18	20	12	50

tion on pheasants (Tab. 4), whereas cats and goshawks were of secondary importance; other predators were unimportant.

Pheasant nests were primarily preyed upon by hooded crows but also by badgers (Tab. 5). Predation by crows was most intense during pheasant egg-laying. During incubation, predation by crows decreased and was similar to that by badgers (Tab. 5).

Other studies have shown that the red fox is a dominant predator on small game in agricultural areas (Dumke and Pils 1973, Goszczynski et al. 1976, Pils and Martin 1978, Potts 1980). The relative importance of the domestic cat as a game predator seems to vary. In Wisconsin feral cats were important predators (Burger 1966), whereas in Poland they were not (Goszczynski et al. 1976, Pielowski 1976b). The goshawk was reported to be an important pheasant predator in another Swedish area (Kenward et al. 1981).

4.4. Predation in relation to production of hares and pheasants

Data indicated that at least 40% of the annual production of hares and almost 60% of subadult and adult pheasants in autumn were consumed by the predators (Tab. 3). However, for several reasons we are hesitant of drawing any firm conclusions about predation as a limiting factor for game populations. First, although our results are based on very large sample sizes, still the amount of remains from game animals is small and therefore uncertain, regarding e.g. seasonal and inter-annual variations. Second, it has been pointed out that short-term studies regarding interspecific relations such as predation and competition are unreliable (Wiens 1977, Kephart and Arnold 1982). Most of our data are from only two years and might not reflect long-term fluctuations in the predation pattern. Third, we do not know to what extent the animals eaten by the predators actually were killed by them, and whether the predators mainly kill individuals predisposed to die (Errington 1946). A study designed to answer that question was performed on snowshoe hare in North America (Brand et al. 1975). They found that all recorded mortality in adult hares (12 radio-tracked individuals) and the main part of deaths among juveniles (9 individuals out of 14) were caused by predators (a.o. lynx, coyote, weasels, goshawk and great horned owl), and there was no evidence that predator-killed hares were in poor condition. Fourth, it is unknown how much prey populations can compensate for predation losses by increased reproductive output. A considerable part of pheasant hens do not breed and this non-breeding fraction is positively correlated with the density of pheasants (Göransson 1980). Therefore increased hen mortality may be compensated for by the nesting of formerly non-breeding hens. In cases of egg-losses during laying or incubation it is known that pheasant hens compensate for these losses by renesting (e.g. Göransson 1980).

Experimental removal of predators is the only adequate method of assessing the impact of predation. During an anti-rabies campaign in Denmark, fox numbers were reduced about 60% in a large area and at the same time the hunting bag of hares and pheasants increased by 50–100% (Jensen 1970, Strandgaard and Asferg 1980). In a study in North America, removal of predators caused a two-fold increase in pheasant hatching success as compared with a control area (Chesness et al. 1968). However, nest density did not increase during the experiment indicating that decreased predation rate had no influence on breeding density. Further, a 60% increase in duckling production was recorded in another predator controlled area (Balser et al. 1968). In a comparative study on recruitments of pheasants and hares on an almost predator-free large island (Ven island) about 40 km from the Revinge area just outside the Swedish coast, the recruitments for these species were approximately twice as high as in the Revinge area (Frylestam 1980, Göransson 1980). Removal of predators in our area would probably increase the hunting bag as in Jensen's study. However, this does not necessarily imply that predators limit the breeding density of hares and pheasants.

Acknowledgements – We thank the late Tom Nilsson for data on polecat numbers and diet, L. Keith and an anonymous referee for valuable comments on the manuscript, M. Andersson for making preparations and analysing hairs, J. Byers for correcting the English and A. Odham for typing the manuscript. Grants were obtained from the Swedish Natural Science Research Council (to S. Erlinge), and the National Swedish Environment Protection Board, (to S. Erlinge and to G. Göransson).

References

Balser, D. S., Dill, H. H. and Nelson, N.K. 1968. Effect of predator reduction on waterfowl nesting success. – J. Wildl. Mgmt. 32: 669–682.

Brand, Ch. J., Vowles, R. H. and Keith, L. N. 1975. Snowshoe hare mortality monitored by telemetry. – J. Wildl. Mgmt. 39: 741–747.

Brunner, H. and Coman, B. 1974. The identification of mammalian hair. – Inkata Press, Melbourne.

Burger, G. U. 1966. Observations on aggressive behavior of male ring-necked pheasants in Wisconsin. – J. Wildl. Mgmt. 30: 57–64.

Chesness, R. A., Nelson, M. M. and Longley, W. H. 1968. The effect of predator removal on pheasant reproductive success. – J. Wildl. Mgmt. 32: 683–697.

Dale, F. H. 1952. Sex ratio in pheasant research and management. – J. Wildl. Mgmt. 16: 156–163.

Day, M. G. 1966. Identification of hair and feather remains in the gut and faeces of stoat and weasel. – J. Zool. Lond. 148: 201–217.

Dumke, R. T. and Pils, C. M. 1973. Mortality of radio-tagged pheasants on the Waterloo wildlife area. – Techn. Bull. No. 72, Dept. Nat. Resources, Madison, Wisconsin. 52 pp.

Erlinge, S. 1981. Food preference, optimal diet and reproductive output in stoats *Mustela erminea* in Sweden. – Oikos 36: 303–315.

– 1983. Demography and dynamics of a stoat *Mustela erminea* population in a diverse community of vertebrates. – J. Anim. Ecol. 52: 705–726.

– , Göransson, G., Hansson, L., Högstedt, G., Liberg, O., Nilsson, I. N., Nilsson, T., Schantz, T. von and Sylvén, M. 1983. Predation as a regulating factor on small rodent populations in southern Sweden. – Oikos 40: 36–52.

Errington, P. L. 1946. Predation and vertebrate populations. – Quart. Rev. Biol. 21: 144, 177, 221–245.

Frylestam, B. 1979. Structure, size, and dynamics of three European hare populations in southern Sweden. – Acta theriol. 24, 33: 449–464.

– 1980. Reproduction in the European hare in southern Sweden. – Holarct. Ecol. 3: 74–80.

– 1981. Estimating by spotlight the population density of the European hare. – Acta theriol. 26, 28: 419–427.

Goszczyński, J., Ryszkowski, L. and Truszkowski, J. 1976. The role of the European hare in the diet of predators in cultivated field systems. – In: Pielowski, Z. and Pucek, M. (eds), Ecology and management of European hare populations. Warszawa, pp. 269–286.

Göransson, G. 1980. Dynamics, reproduction and social organization in pheasant *Phasianus colchicus* populations in South Scandinavia. – Ph.D. Thesis, Lund.

Jensen, B. 1970. Effect of a fox control programme on the bag of some other game species. – Trans. Congr. Game Biol. IX, pp. 480.

Keith, L. B. 1974. Some features of population dynamics in mammals. – Proc. Int. Congr. Game Biol. XI. pp. 17–58.

– , Todd, A. W., Brand, Ch. J., Adamcik, R. S. and Rusch, D. H. 1977. An analysis of predation during a cyclic fluctuation of snowshoe hares. – Proc. Int. Congr. Game Biol. XIII, pp. 151–175.

Kenward, R. E., Marcström, V. and Karlbom, M. 1981. Goshawk winter ecology in Swedish pheasant habitats. – J. Wildl. Mgmt. 45: 397–408.

Kephart, D. G. and Arnold, S. J. 1982. Garter snake diets in a fluctuating environment: A seven-year study. – Ecology 63: 1232–1236.

Kimball, J. W. 1949. The crowing count pheasant census. – J. Wildl. Mgmt. 13: 101–120.

Liberg, O. 1981. Predation and social behaviour in a population of domestic cat. – Ph.D. Thesis, Lund.

– 1982. Correction factors for important prey categories in the diet of domestic cats. – Acta theriol. 27: 115–122.

Nilsson, I. N. 1981. Ecological aspects on birds of prey, especially long-eared owl and tawny owl. – Ph.D. Thesis, Lund.

Pielowski, Z. 1976a. The role of foxes in the reduction of the European hare population. – In: Pielowski, Z. and Pucek, M. (eds), Ecology and management of European hare populations. Warszawa 1976, pp. 135–148.

– 1976b. Cats and dogs in the European hare hunting ground. – In: Pielowski, Z. and Pucek, M. (eds), Ecology and management of European hare populations. Warszawa. pp. 153–156.

Pils, C. M. and Martin, M. A. 1978. Population dynamics, predator-prey relationships and management of the red fox in Wisconsin. – Techn. Bull. No. 105, Dept. Nat. Resources, Madison, Wisconsin. 56 pp.

Potts, G. R. 1980. The effects of modern agriculture, nest predation and game management on the population ecology of partridges (*Perdix perdix* and *Alectoris rufa*). – Adv. Ecol. Res. 11: 2–79.

Schantz, T. von 1980. Prey consumption of a red fox population in southern Sweden. – In: Zimen, E. (ed.), The red fox. Biogeographica; vol. 18, Junk, The Hague, pp. 53–64.

– 1981. Evolution of group living, and the importance of food and social organization in population regulation; a study on the red fox (*Vulpes vulpes*). – Ph.D. Thesis, Lund.

Strandgaard, H. and Asferg, T. 1980. The Danish bag record II. – Dan. Rev. Game Biol. 11. 112 pp.

Sylvén, M. 1982. Reproduction and survival in Common Buzzards (*Buteo buteo*) illustrated by the seasonal allocation of energy expenses. – Ph.D. Thesis, Lund.

Wagner, H. W., Besadny, C. D. and Kabat, C. 1965. Population ecology and management of Wisconsin pheasants. – Techn. Bull. No. 34, Dept. Nat. Resources, Madison, Wisconsin. 168 pp.

Wiens, J. A. 1977. On competition and variable environments. – Am. Scientist 65: 590–597.