

- LEHNER, P. N. (1978): Coyote communication. In: Coyotes, Biology, Behaviour and Management. Ed. by M. BEKOFF. New York: Academic Press. 127-162.
- LEISTNER, O. A. (1967): The plant ecology of the southern Kalahari. Mem. bot. Surv. S. Afr. **38**, 1-172.
- MACDONALD, D. W. (1979a): Some observations and field experiments on the urine marking behaviour of the red fox, *Vulpes vulpes*. Z. Tierpsychol. **51**, 1-22.
- (1979b): The flexible social system of the golden jackal, *Canis aureus*. Behav. Ecol. Sociobiol. **5**, 17-38.
- (1980): Patterns of scent marking with urine and faeces amongst carnivore communities. Symp. zool. Soc. Lond. **45**, 107-139.
- MILLS, M. G. L. (1978): Foraging behaviour of the brown hyaena (*Hyaena brunnea* Thunberg, 1820) in the southern Kalahari. Z. Tierpsychol. **48**, 113-141.
- NEL, J. A. J. (1978): Notes on the food and foraging behavior of the bat-eared fox *Otocyon megalotis*. Bull. Carnegie Mus. Nat. Hist. **6**, 132-137.
- PETERS, R. P.; MECH, L. D. (1975): Scent-marking in Wolves. Am. Scient. **63**, 628-637.
- ROTHMAN, R. J.; MECH, L. D. (1980): Scent-marking in lone wolves and newly formed pairs. Anim. Behav. **27**, 750-760.
- SCHENKEL, R. (1947): Ausdrucks-Studien an Wölfen. Behaviour **1**, 81-129.
- SKEAD, D. M. (1973): Incidence of calling in the black-backed jackal. J. sth. Afr. Wildl. Mgmt Ass. **3**, 28-29.
- WELLS, M. C.; BEKOFF, M. (1981): An observational study of scent-marking in coyotes, *Canis latrans*. Anim. Behav. **29**, 322-350.

*Authors' address:* J. A. J. NEL and M. H. BESTER, Mammal Research Institute, University of Pretoria, 0002 Pretoria, South Africa

## Behaviour of an expanding population of the Brown bear (*Ursus arctos*) in northern Europe

By E. PULLIAINEN

*Department of Zoology, University of Oulu*

*Receipt of Ms. 27. 1. 1983*

### Abstract

The behaviour of a brown bear population (*Ursus arctos*) in N Europe was studied in the years 1968-1982 with the help of the Finnish Border Patrol Establishment and local hunters. Finland received an immigration of bears in the 1970s and the early 1980s from the saturated Soviet Karelian population (approx. 3000 ind. around 1980). Continued immigration from Soviet Karelia into Finnish Northern Karelia, Kainuu and Koillismaa caused the bears to move on into the inland areas of Finland, some crossing the whole country from east to west. Bears also appeared in the southeastern frontier area of Finland, and some slight immigration was recorded from the Kola Peninsula into eastern Finnish Lapland. Finland received 682 bears more from its neighbouring countries (mainly Soviet Karelia) than it lost to these countries in the years 1969-1981, a period during which at least 456 bears were killed in Finland. The number of bears in Finland thus increased by about two hundred (to 300-350) during this period. The bears killed in eastern Finland were predominantly males (64.1 % in 1960-1981), and the proportion of cubs killed was 17.8 %. It is assumed that intraspecific aggressiveness (leading especially to sub-adult dispersal) results in emigration, the males being more mobile than the females.



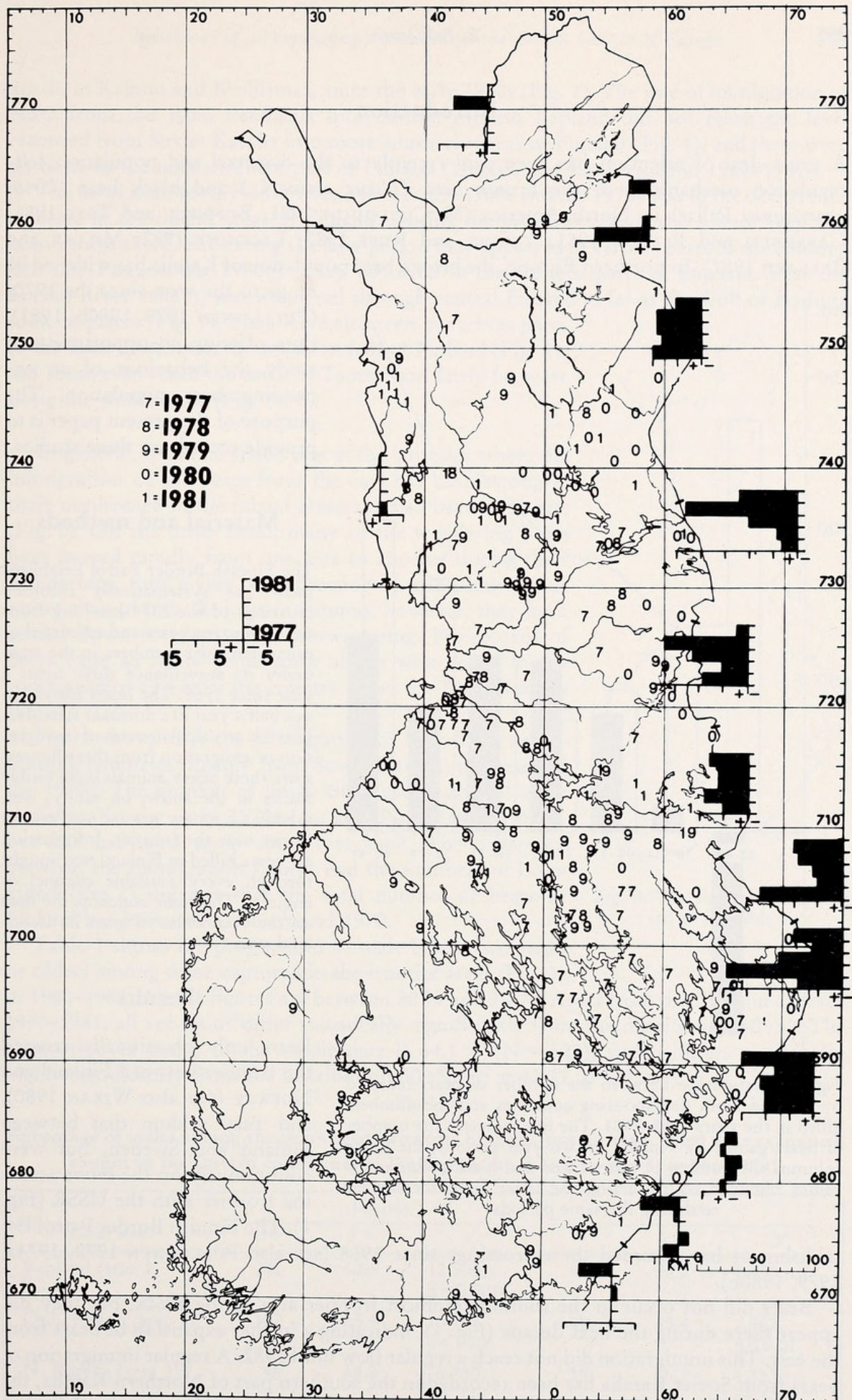


Fig. 1. Numbers of brown bears gained and lost by Finland due to wandering according to the reports of the Finnish Border Patrol Establishment, and places of occurrence of bears in the inland area according to newspaper and other reports during the same period



## Introduction

A great deal of attention has been paid recently to the dispersal and population self-regulation mechanisms of the brown bear (*Ursus arctos* L.) and black bear (*Ursus americanus* Pallas) in North America (McCULLOUGH 1981; BUNNELL and TAIT 1981; GARSHELIS and PELTON 1981; YOUNG and RUFF 1982; LECOUNT 1982; MILLER and BALLARD 1982). In northern Europe, the brown bear population of Karelia has widened its

range to the west since the 1970s (PULLIAINEN 1979, 1980b, 1981), thus offering an opportunity to study the behaviour of an expanding bear population. The purpose of the present paper is to provide records on these studies.

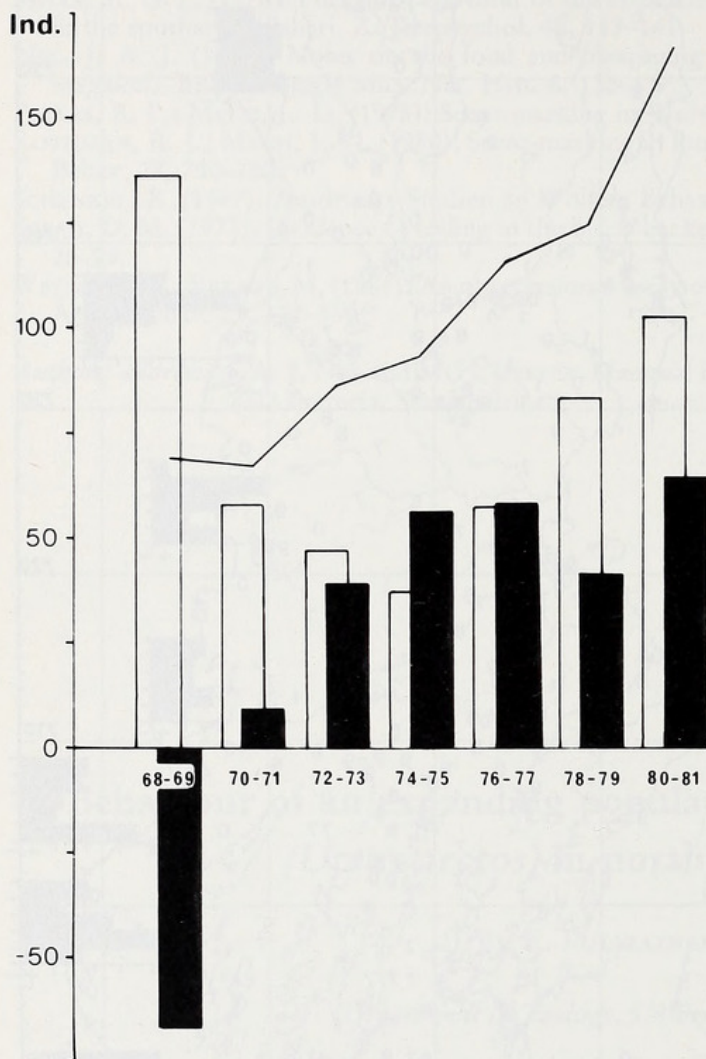


Fig. 2. Relationship between the number of bears received by Finland from neighbouring countries and the numbers killed in the years 1968-1981. The line indicates the number of bears gained by Finland in two-year periods, the white columns the number of bears killed and black columns the values obtained by deducting the latter from the former during the same periods

establishment has recorded these crossings since 1968 (see also PULLIAINEN 1972, 1974a, 1979, 1980b).

Bears did not occur in the southeasternmost frontier area in the 1960s, but they did appear there during the next decade (Fig. 1), indicating a further expansion of bears from the east. This immigration did not reach a regular flow until 1982. A regular immigration of bears from Soviet Karelia has been recorded in the southern part of Northern Karelia, the next frontier area to the north, since the late 1970s, and in the northern part and further

## Material and methods

The Finnish Border Patrol Establishment has systematically recorded crossings of the 2574-km-long frontier by brown bears and estimated or calculated their numbers in the areas under its surveillance three times a year since 1968. The bears spend about half a year in a dormant state. It is possible to calculate rates of immigration or emigration from these figures, since these heavy animals leave visible tracks in the snow, on sandy, wet, muddy or mossy ground and on the fences near the frontier. Information on bears killed in Finland was sought through every available channel of enquiry. The same concerns the data on the occurrence of bears in the inland area.

## Results

Bears only occasionally crossed the frontier between Finland and Norway (see also WIKAN 1980), and very seldom that between Finland and Sweden, but were continuously on the move across the frontier with the USSR (Fig. 1). The Finnish Border Patrol Es-



north, in Kainuu and Koillismaa, since the early 1970s (Fig. 1). The rate of immigration of bears from the Kola Peninsula into eastern Finnish Lapland did not reach the level recorded from Soviet Karelia into more southerly areas of Finland (Fig. 1), and there were no bears in the northernmost part of Finland (Utsjoki and Enontekiö) in 1968–1981.

The most noteworthy difference between the 1960s and the 1970s was in the occurrence of bears in the inland areas of Finland. During the previous decade there were very few occurrences there, but during the later period they appeared in various parts of the country (see also PULLIAINEN 1980b). They occurred in the western parts of Lapland (near the Tornio River valley), and wandered through central Finland as far as the Gulf of Bothnia coast in places (Fig. 1). They were also seen in various parts of the Lake District in the southern half of Finland (Fig. 1), and some even reach the town of Tammissaari fairly far west along the south coast (Fig. 1).

In general, it can be stated that at the latitudes where the immigration of the bears from the east has been strongest their occurrence in the inland areas has also been strongest (Fig. 1). On the other hand, many of the wandering bears have moved rapidly from one area to another during their wanderings, thus giving an impression of many individuals rather than of one. At least in autumn, however, they have settled down to prepare for overwintering. No records of bears exist so far in some parts of the west coast, in the southwestern corner of the country or on the Åland Islands (Fig. 1).

Fig. 2 shows that the immigration of bear from neighbouring countries (mainly from Soviet Karelia) increased in the 1970s. The number of bears killed each year was at its minimum in the early 1970s (see also PULLIAINEN 1980a), but has increased again since that time. The difference between the immigration figures and the numbers of bears killed (Fig. 2) suggests that the total number of bears in Finland has increased since around 1970.

Table 1 shows the proportions of male bears (two years or older) among those captured in the frontier areas (Fig. 3) in 1960–1981. All the figures are between 58% and 70%. Apart from the Lapland data for 1970–1981, all sex ratios differ statistically significantly from the distribution 50:50. The proportion of males in the whole data is 64.1% (N = 523), which differs statistically highly significantly from the distribution 50:50 ( $\chi^2 = 41.31$ ,  $p < 0.001$ ).

Table 1

Percentage of males among the bears aged two years or older (not all bears killed were examined) caught in the eastern communes of Finland (areas shown in Fig. 3) in 1960–1981

Study areas	1960–1969			1970–1981		
	N	♂ %	$\chi^2$	N	♂ %	$\chi^2$
Lapland (area 1)	200	62.5	12.500, $p < 0.001$	80	58.8	2.450, ns
Oulu region (area 2)	107	65.4	10.178, $p < 0.01$	49	69.4	7.367, $p < 0.01$
N. Karelia (area 3)	48	68.8	6.750, $p < 0.01$	39	66.7	4.333, $p < 0.05$

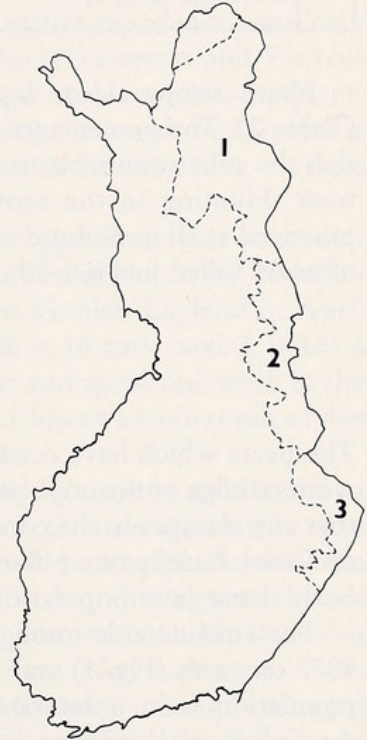


Fig. 3. The study areas referred to in Table 1



Table 2

Percentage of cubs among those bears killed in Finland in 1960–1981 which were examined for age  
The areas are shown in Fig. 3

Areas	1960–1969		1970–1981	
	No. of cubs	%	No. of cubs	%
Lapland (area 1)	62	18.7	29	22.8
Oulu region (area 2)	13	9.7	1	1.8
N. Karelia (area 3)	1	1.7	5	10.6

Major temporal and local variations have occurred in the proportion of cubs killed (Table 2). The percentages were highest in eastern Lapland, which may be due to the fact that the cubs are unable to escape hunters in the snow in spring and can be easily shot from trees. Hunting in the snow conditions is not so common further south, and it is not practiced at all in Kuhmo or Northern Karelia. The proportion of cubs in the total number of bears killed in 1960–1981 was 17.8 %.

### Discussion

The bears which have occurred in Finland in the period 1960–1981 actually represent the western edge of the population inhabiting the northern European USSR. It can be expected that any changes in the core of the population will also be reflected at its edges. In the case of Soviet Karelia one possible direction for emigration is Finland, since there are already fairly dense bear populations in the north and south, and the White Sea lies to the east.

The considerable immigration of bears into Finland from Soviet Karelia from around 1970 onwards (Fig. 1) may be due either to population pressure (when the adjacent Soviet population is in a saturated state) or to changes in the prevailing natural conditions. According to the studies of Dr. P. I. DANILOV (pers. comm.), the number of bears in Soviet Karelia in 1980 was approx. 3000 individuals.

Natural mortality among adult bears is usually rather low in a saturated population, with the result that a high percentage of the population are of breeding age (LECOUNT 1982). NOVIKOV et al. (1969) report that 13.8 % of the Soviet Karelian bear population were younger than one year, while the proportion of cubs among those killed in eastern Finland in 1960–1981 was 17.8 %. The proportion of cubs in a saturated grizzly bear population in the Yellowstone National Park was 15 % (McCULLOUGH 1981).

An average of 150 bears per year were killed by humans in Soviet Karelia in the 1970s (P. I. DANILOV, pers. comm.). Using a figure of 14 % cubs, there would be a little over 400 cubs in the first summer, while a figure of 18 % would give over 100 cubs more. All these calculations suggest a yearly extra recruitment which must be accounted for by death or dispersal, assuming that the population is in a saturated state.

Three mechanisms are known to be important in regulating bear numbers, namely nutrition, sub-adult dispersal and cannibalism. Evidence of each of these has been recorded (see reviews in McCULLOUGH 1981; YOUNG and RUFF 1982). There were no total failures in berry crops in Soviet Karelia in the 1970s which might have caused mass movements of bears. Wandering by starving bears have been observed earlier in Manchuria (RAKOV 1966) and in Irkutsk (GUDRITIS 1963). Adult males may kill both cubs (e.g. TROYER and HENSEL 1962; COLE 1973, CRAIGHEAD 1979) and sub-adults (e.g. ERICKSON 1957; BLACK 1958; JONKEL and COWAN 1971; BEECHAM 1980; LECOUNT 1982), but we have no corresponding records from Finland so far, although this does not mean that such things could not occur here.



Many recent studies suggest that sub-adult dispersal is an important factor in regulating bear numbers (e.g. YOUNG and RUFF 1982; LECOUNT 1982; MILLER and BALLARD 1982). Sub-adult and adult males travel more extensively than their female counterparts (ROGERS 1977; ALT et al. 1980; LECOUNT 1980, 1982; REYNOLDS and BEECHAM 1980), and thus may both increase their vulnerability to killing by humans (see LECOUNT 1982), and also lead to emigration.

YOUNG and RUFF (1982) found that there was a greater tendency for sub-adult black bears to move away from the study area rather than adults, and concluded that adult males may influence sub-adult dispersal, although without actually excluding them from their home ranges. YOUNG and RUFF (1982) assume that sub-adult males recognize the dominance and potential threat of larger adults on the basis of their earlier experiences, and may subsequently either avoid habitats preferred by the adult males (GARSHELIS and PELTON 1981) or disperse to areas where direct encounters with larger males are less frequent. BUNNELL and TAIT (1981) also conclude that aggression by adult males of the Ursidae is directed towards the sub-adult males, resulting in the eviction of the latter or their voluntary evacuation from an area.

We have some direct and some indirect support for the hypothesis that sub-adult dispersal may play an important role in the emigration of bears from the Soviet Karelian population. Our field team observed an actual case in eastern Finnish Lapland in April 1979 (PULLIAINEN et al. 1979), in which large bear (track  $26 \times 16$  cm), having killed a moose (*Alces alces*), drove a smaller bear away from the carcass and spent one week in the immediate vicinity itself. The smaller individual moved some 3.1 km away as a result of this first escape and did not return to the carcass during that week.

ROGERS (1977), ALT et al. (1980), LECOUNT (1980, 1982) and REYNOLDS and BEECHAM (1980) have all found that sub-adult (and also adult) males travel more extensively than their female counterparts. It is thus to be expected that there will be a surplus of males in the marginal populations. As a background to this, it is worth remembering that the sex ratio of newly born bear cubs (in a zoo) is even (DITTRICH and KRONBERGER 1963), as also is that of bears younger than one year under natural conditions (NOVIKOV et al. 1969; PULLIAINEN 1972). In the present case a surplus of males was recorded among bears aged two years or older shot in the areas adjacent to the Soviet territory (Table 1). If the bears had left Soviet Karelia due to habitat destruction, e.g. clear-cutting of forests, the sexes might have been expected to be equally represented among the emigrating individuals.

Bears have occurred in Northern Karelia, Kainuu and Koillismaa, adjacent to the eastern frontier of Finland, throughout this century, but the population density has been rather low and only occasionally have any individuals wandered further inland. In this respect the situation in recent years has been different, since considerable numbers of bears have continued westwards, even crossing the whole country, e.g. to the vicinity of Oulu on the west coast (Fig. 1). The ultimate cause of this behaviour must lie in population pressure maintained by a continuous immigration of bears from the east (Fig. 1). The rate of movements to the west has been greatest at the latitude where immigration from the east has been greatest (Fig. 1).

The recent invasion of bears into central and southern parts of Finland has taken place in the settled part of the country. In many cases the bears have moved rapidly from one village and region to another. The reason for this behaviour must be interference from humans, their vehicles and other constructions. The bears of the eastern forests have not become familiar with man in their original habitat, and tend to avoid contacts, but they are capable of adapting to the presence of humans, as the well-known examples of the national parks in the USA show. In Finland some of the wandering bears have settled in the various parts of the southern half of the country.

The distances covered by the bears during their wanderings in Finland are in no way exceptional. When 47 brown bears were captured and transplanted in Alaska, USA



(MILLER and BALLARD 1982), at least 12 of the 20 adults successfully returned from an average transplant distance of 198 km. Most bears were aware of the correct homing direction, i.e. they were able to orient themselves like polar bears (*Ursus maritimus*) (LENTFER 1972, 1973). The return of so many bears indicates the importance of a familiar area in the life of the brown bear, as in that of many other mammals (see PULLIAINEN 1974b, 1982b; BAKER 1978).

Since the Second World War Finland has received two major immigrations of wolves from the east (PULLIAINEN 1965, 1980c, 1982a), but there seems to be an obvious difference between the wandering patterns of the wolf and the bear. The wolf uses specific migration routes, which often consist of ridges and corresponding formations along which it is easy to travel (PULLIAINEN 1965, 1980c), while the bear will even go through dense forests and thickets which are difficult to penetrate, but which at the same time offer good shelter.

Finland received 682 bears more from its neighbouring countries (mainly from Soviet Karelia) than it lost to these countries in the years 1969–1981, a period during which at least 456 bears were killed in Finland (PULLIAINEN 1980a, unpubl. data). Taking the natural population increase and mortality rates into consideration, it can be expected that the number of bears in Finland will have increased by about two hundred during this period. The estimates serve to confirm this impression, since the population in the areas under the surveillance of the border patrols appears to have increased by about 110 individuals between 1968 and 1982, in addition to which many bears have wandered further inland in both Lapland and Central and Southern Finland (Fig. 1). There were 300–350 bears in Finland in autumn 1982.

#### Acknowledgements

The author wishes to express his sincere gratitude to the staff of the Finnish Border Patrol Establishment for its technical assistance in the field.

This paper constitutes Report No. 138 from the Värriö Subarctic Research Station of the University of Helsinki.

#### Zusammenfassung

##### *Zum Verhalten des expandierenden Bärenbestandes (Ursus arctos) in Nordeuropa*

Das Verhalten des Bärenbestandes (*Ursus arctos*) wurde in Nordeuropa in den Jahren 1968–1982 mit Unterstützung des finnischen Grenzbewachungswesens und örtlicher Jäger untersucht. Finnland war in den siebziger und Anfang der achtziger Jahre Ziel einer Bärenimmigration der saturierten Population Russisch-Kareliens (ca. 3000 Tiere um 1980). Die fortgesetzte Immigration aus Russisch-Karelien nach Finnisch-Nordkarelien, Kainuu und Koillismaa hatte eine Wanderung der Bären von der Grenznähe ins Landesinnere, sogar quer durch das Land von Osten nach Westen, zur Folge. Bären erschienen auch an der Südostgrenze Finnlands und eine geringere Immigration wurde von der Halbinsel Kola nach Finnisch-Ostlappland beobachtet. Nach Finnland wanderten 682 Bären mehr ein als es in den Jahren 1968–1981 an seine Nachbarländer verlor. In diesem Zeitraum wurden in Finnland mindestens 456 Bären erlegt. Somit wuchs der Bärenbestand Finnlands im Laufe dieses Zeitraums um etwa 200 Bären (auf 300–350 Tiere) an. Von den in Ostfinnland erlegten Bären waren die Mehrheit (64,1 % in den Jahren 1960–1981) männliche Tiere, der Anteil der erlegten Jungtiere war 17,8 %. Es wird angenommen, daß die innerartliche Aggressivität der Spezies zur Emigration besonders von heranwachsenden Tieren führt, wobei männliche Tiere beweglicher sind als weibliche.

#### References

- ALT, G. L.; MATULA, G. J. Jr.; ALT, F. W.; LINDZEY, J. S. (1980): Dynamics of home range and movements of adult black bears in northeastern Pennsylvania. In: Bears – Their Biology and Management. Ed. by C. J. MARTINKA, K. L. MACARTHUR. Bear Biology Ass. 131–136.
- BAKER, R. R. (1978): The Evolutionary Ecology of Animal Migration. London: Hodder and Stoughton.
- BEECHAM, J. J. (1980): Some population characteristics of two black bear populations in Idaho. In: Bears – Their Biology and Management. Ed. by C. J. MARTINKA, K. L. MACARTHUR. Bear Biology Ass. 201–204.
- BLACK, H. C. (1958): Black bear research in New York. Trans. North Am. Wildl. Conf. 23, 443–461.
- BUNNELL, F. L.; TAIT, D. E. N. (1981): Population Dynamics of Bears – Implications. In: Dynamics of Large Mammal Populations. Ed. by C. W. FOWLER, T. D. SMITH. New York: John Wiley & Sons. 75–98.



- COLE, G. F. (1973): Management involving grizzly bears in Yellowstone National Park 1970-72. U. S. Dept. of Interior, Natl. Park. Serv., Nat. Resour. Rep. 7, 1-10.
- CRAIGHEAD, F. C. Jr. (1979): Track of the Grizzly. San Fransisco: Sierra Club Books.
- DITTRICH, L.; KRONBERGER, H. (1963): Biologisch-anatomische Untersuchungen über die Fortpflanzungsbiologie des Braunbären (*Ursus arctos* L.) und anderer Ursiden in Gefangenschaft. Z. Säugetierkunde 28, 129-155.
- ERICKSON, A. W. (1957): Techniques for live-trapping and handling black bears. Trans. North Am. Wildl. Conf. 22, 520-543.
- GARSHELIS, D. L.; PELTON, M. R. (1981): Movements of black bears in the Great Smoky Mountains National Park. J. Wildl. Manage. 45, 912-925.
- GUDRITIS, V. E. (1963): O medved'ah-šatunah v vostočnoj Sibiri. Zool. Žurnal 42, 960-961.
- JONKEL, C. J.; COWAN, I. M. (1971): The black bear in the spruce-fir forest. Wildl. Monogr. 27, 1-57.
- LECOUNT, A. L. (1980): Some aspects of black bear ecology in the Arizona chaparral. In: Bears - Their Biology and Management. Ed. by C. J. MARTINKA, K. L. MACARTHUR. Bear Biology Ass. 175-180.
- LECOUNT, A. L. (1982): Characteristics of a central Arizona black bear population. J. Wildl. Manage. 46, 861-868.
- LENTFER, J. W. (1972): Polar bear-sea ice relationships. In: Bears - Their Biology and Management. Ed. by S. HERRERO. Morges: IUCN 165-171.
- LENTFER, J. W. (1973): Discreteness of Alaskan polar bear populations. Proc. Int. Congr. Game Biol. 11, 323-329.
- MCCULLOUGH, D. R. (1981): Population Dynamics of the Yellowstone Grizzly Bear. In: Dynamics of Large Mammal Populations. Ed. by C. W. FOWLER, T. D. SMITH. New York: John Wiley & Sons. 173-196.
- MILLER, S. D.; BALLARD, W. B. (1982): Homing of transplanted Alaskan brown bears. J. Wildl. Manage. 46, 869-876.
- NOVIKOV, G. A.; AIRAPET'JAN, A. E.; PUKINSKIJ, JU. B.; TIMOFEEVA, E. K.; FOKIN, I. M. (1969): Nekotorye osobennosti populacii buryh medvedej Leningradskoj oblasti. Zool. Žurnal. 48, 885-901.
- PULLIAINEN, E. (1965): Studies on the wolf (*Canis lupus* L.) in Finland. Ann. Zool. Fennici 2, 215-259.
- PULLIAINEN, E. (1972): Distribution and population structure of the bear (*Ursus arctos* L.) in Finland. Ann. Zool. Fennici 9, 199-207.
- PULLIAINEN, E. (1974a): Suomen suurpedot. Helsinki: Tammi.
- PULLIAINEN, E. (1974b): Seasonal movements of moose in Europe. Naturaliste can. 101, 379-392.
- PULLIAINEN, E. (1979): Erfarenheter av uppföljning av de stora rovdjuren i Finland. Viltrappport 9, 60-70.
- PULLIAINEN, E. (1980a): The number of bear (*Ursus arctos*) and lynx (*Felis lynx*) killed in Finland in 1973-1976. Suomen Riista 28, 67-70.
- PULLIAINEN, E. (1980b): Ensuring the survival of the great predators in Finland. Luonnon Tutkija 84, 111-112, 159-160.
- PULLIAINEN, E. (1980c): The status, structure and behaviour of populations of the wolf (*Canis l. lupus* L.) along the Fenno-Soviet border. Ann. Zool. Fennici 17, 107-112.
- PULLIAINEN, E. (1981): History of the great predators in Finland. Tiede 2000, 1981, 21-25, 51.
- PULLIAINEN, E. (1982a): Behavior and Structure of an Expanding Wolf Population in Karelia, Northern Europe. In: Wolves of the World. Perspectives of Behavior, Ecology, and Conservation. Ed. by F. H. HARRINGTON, P. C. PAQUET. 134-145.
- PULLIAINEN, E. (1982b): Use of the home range by pine martens (*Martes martes* L.). Acta Zool. Fenn. 172 (in press).
- PULLIAINEN, E., HIETAJÄRVI, T.; IVANAINEN, J.; LAITINEN, M.; VAARALA, K. (1979): Springtime news about bears. Suomen Luonto 38, 179-181, 191.
- RAKOV, N. V. (1966): Ob osobennost'ah sosysčestvovani' a kabana burogo i černogo medvedej v Amuro-ussurijskom krae. Zool. Žurnal. 45, 617-618.
- REYNOLDS, D.; BEECHAM, J. J. (1980): Home range activities and reproduction of black bears in west-central Idaho. In: Bears - Their Biology and Management. Ed. By. C. J. MARTINKA, K. L. MACARTHUR. Bear Biology Ass. 181-190.
- ROGERS, L. L. (1977): Social relationships, movements, and population dynamics of black bears in northeastern Minnesota. Minneapolis: Univ. Minnesota.
- TROYER, W. A.; HENSEL, R. J. (1962): Cannibalism in brown bear. Anim. Behav. 10, 231.
- WIKAN, S. (1980): Verhaltensbiologische und ökologische Beobachtungen am Braunbären (*Ursus arctos* L.) im Pasvik-Tal, Norwegen. Cour. Forsch.-Inst. Senckenberg 38, 1-77.
- YOUNG, B. F.; RUFF, R. L. (1982): Population dynamics and movements of black bears in east central Alberta. J. Wildl. Manage. 46, 845-860.

Author's address: Prof. Dr. ERKKI PULLIAINEN, Department of Zoology, University of Oulu, Kasarmintie 8, SF-90100 Oulu 10, Finland





Pulliainen, Erkki. 1982. "Behaviour of an expanding population of the Brown bear (*Ursus arctos*) in northern Europe." *Zeitschrift für Säugetierkunde : im Auftrage der Deutschen Gesellschaft für Säugetierkunde e.V* 48, 290–297.

**View This Item Online:** <https://www.biodiversitylibrary.org/item/163244>

**Permalink:** <https://www.biodiversitylibrary.org/partpdf/191657>

#### **Holding Institution**

Smithsonian Libraries and Archives

#### **Sponsored by**

Biodiversity Heritage Library

#### **Copyright & Reuse**

Copyright Status: In Copyright. Digitized with the permission of the rights holder.

Rights Holder: Deutsche Gesellschaft für Säugetierkunde

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://www.biodiversitylibrary.org/permissions/>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.