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Authors: Kojola, Ilpo, Hallikainen, Ville, Heikkinen, Samuli, and Nivala, Vesa

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Inadvertent shooting of brown bear cubs in Finland: what can managers do to reduce it?

Ilpo Kojola, Ville Hallikainen, Samuli Heikkinen and Vesa Nivala

I. Kojola ✉ (ilpo.kojola@luke.fi), V. Hallikainen and V. Nivala, Natural Resources Institute Finland (Luke), Rovaniemi, Finland. – S. Heikkinen, Natural Resources Institute Finland (Luke), Oulu, Finland.

Family groups with cubs-of-the-year (cubs) in Finland's brown bear *Ursus arctos* population are protected from hunting, but sport hunters inadvertently shoot some cubs almost every year. In our data, 39 of 1463 bears from hunting bags (and 39 of all 1503 shot bears) during 1996–2018 were cubs. Mortality of cubs owing to inadvertent shooting by hunters was estimated to be relatively low (ca 8%) and was therefore above all an ethical problem. Male bias from the 1:1 sex ratio was significant (67%, $\chi^2 = 4.333$, $p = 0.037$) and possibly attributed to a greater resemblance with yearlings (legal game) given their larger body size. The year trend in the proportion of cubs in hunting bag was not significant ($t = -1.832$, $p = 0.076$). We examined whether the risk of cub to being killed by hunters was related to the distance from the Russian border because bear hunting has been practised for more years in eastern Finland compared with mid- and western Finland. The risk of cub being killed was not related to the distance but the risk of female cubs being killed was highest within a narrow zone at the Russian border. If the family group escapes to the Russian side, the risk of losing the hunting dog is presumably high. Given hunters' high motivation to keep their valuable bear-hunting dogs, the proportion of female cubs might be highest near the border. Systematic educational programs for hunters would likely reduce the risk of inadvertent killing of cubs. The full legal protection of all family groups is potentially the most efficient method to reduce the risk and thereby formally provide improved ethics in bear hunting. However, this practice might also prolong the mother–offspring bond.

Keywords: inadvertent shooting, hunting, brown bear, cub, management

Recreational hunting is the primary method of regulating some populations of brown bear *Ursus arctos* in Europe (Swenson and Sandegren 1996, Kojola and Heikkinen 2006, Bischof et al. 2008, Huber et al. 2008, Krofel et al. 2012, Bragina et al. 2015, Swenson et al. 2017, Kojola et al. 2020). Hunting is typically limited by season and a quota, but more refined regulations aimed at selective harvesting may also exist. For example, in Slovenia, it is illegal to shoot females with offspring, but it is legal to shoot the dependent cubs (Krofel et al. 2012). In Sweden, both females and dependent cubs are protected from hunting (Bischof et al. 2008). In Finland, however, legal protection only protects family groups with cubs-of-the-year (hereafter termed cubs). Legal protection of cubs does not provide comprehensive protection, as sport hunters inadvertently shoot cubs they mistake for yearlings, but at least in Sweden, these events are extremely rare (Van de Walle et al. 2018).

Young brown bears attain independence from their mother at the age of 1–2 years in Europe. Males are the dispersing sex, moving away from their mothers (Støen et al. 2006). In contrast, females typically stay near their mothers and may have home ranges that overlap their mothers' home ranges (Ordiz et al. 2008). Cubs are dependent on their mother and share the winter den with her (Dahle and Swenson 2003).

The survival rate among brown bear cubs was traditionally assumed to be very high. However, according to scientific evidence, survival during the first year has been estimated to be only 60–70% in North America (Bunnell and Tait 1985) and 65% in southern Sweden (Swenson et al. 2001). Cub mortality is typically due to intraspecific predation, especially by infanticidal males (Hrdy 1979, Swenson et al. 2001). In hunted bear populations, hunter-caused cub mortality might be a noteworthy factor affecting mortality, although this factor has not been noted in the scientific literature. LeCount (1987) assumed that in the Arizonan black bear population, it is an additive rather than compensatory factor, but the data only included 23 cubs.

The recovery of Finland's brown bear population started in approximately 1970. Since then, the population has been

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increasing and is currently approximately 10-fold more abundant (2300–2500 bears) than in the late 1970s (Pul-liainen 1990, Kojola and Heikkinen 2006, Kopatz et al. 2019, Heikkinen et al. 2020). Sport hunting of bears has gradually become more popular, and the harvest has been increasing and has spread to more peripheral regions than merely the population core (Kojola et al. 2020). From the early 1990s, the Hunters' Central Organization and Finnish Hunter Association began organizing bear hunting courses and distributing educational material about bear hunting, which increased hunter proficiency. Therefore, we examined whether the kill risk for cubs has declined over time and whether it was lower in core areas where hunters are the most experienced due to having engaged in bear hunting for more years. We investigated whether the proportion of cubs shot is lower in easternmost Finland, where bear hunting has been practised for the longest duration, than in middle and western Finland.

We might expect a male bias in hunter-killed cubs due to the larger body size of males (Dahle et al. 2003 for sex difference in yearlings in the spring). Kojola et al. (2020) found that the sex ratio of older bears is not correlated with the distance from the expected population core areas in Russia. However, the rapid increase in genetic diversity (Hagen et al. 2015) provides evidence of the substantial emigration of bears from Russia to Finland, and migration is usually male biased in brown bears (Støen et al. 2006). In addition, males disperse farther from their mothers' home ranges than females (Støen et al. 2006). However, in the core area of bear hunting in Finland, which is near the eastern border, the annual quota is usually met within a few weeks (<https://riista.fi/metsastys/saalis seuranta/karhusaaliit>), presumably due to the presence of a large number of hunters, and enhanced competition and negligence among hunters may increase the relative risk of female cubs being killed by hunters.

Our research aimed to estimate the proportion of cubs among the harvested bears and to investigate whether this proportion was affected by year (1996–2018), sex and the distance from the Russian border. Based on the results, we discuss how managers could reduce the risk of the inadvertent killing of cubs by hunters.

Material and methods

Study area

Our study area was Finland, which is almost entirely in the boreal forest zone (Ahti et al. 1968). The topography is relatively flat, mostly ranging between 100 and 300 m asl. The dominant tree species are Norway spruce *Picea abies* and Scotch pine *Pinus sylvestris*. Lakes and bogs are regular elements in the landscape. Human densities within bears' home ranges are usually less than 3 people per km². Most forests are commercially used for pulp and timber production. A dense network of forest roads has been constructed to enable forest harvesting. These roads are trafficable by cross-country vehicles and provide bear hunters access into the bears' home ranges.

Harvest rates in Finland's brown bear population are regulated by regional quotas issued by the Ministry of Agricul-

ture and Forestry. Quotas are set annually and are principally based on the volume of damage caused by bears, population estimates and harvest scenarios produced by the Natural Resources Institute Finland (Luke, see Heikkinen et al. 2020).

Data

Our data consisted of 39 cubs and 228 yearlings shot during bear hunting seasons (from 20 August through 31 October) from 1996 to 2018 (Fig. 1) in Finland among a total hunting bag of 1463 bears with known age, sex and location of death. From the total number of bears shot during these hunting seasons ($n = 1503$), two yearlings and 38 older bears were excluded from the analysis because they were shot under the auspices of special licences issued with the purpose of removing a specific individual. All cubs were killed inadvertently, but yearlings were shot legally. The 1996 hunting season was the first season for which the ages of the hunted bears were determined.

Hunters provide the kill site and sex of the bear they have shot in a form for hunted bears and send the second molar to Natural Resources Institute Finland. This practice is not obligatory, but the tooth was sent from > 90% of the harvested bears. The proportion was lower for bears harvested in the reindeer husbandry area in northern Finland. Age was determined at Matson's Laboratory (Montana, USA) based on cementum annuli in the second molar.

Statistical analysis

All statistical analyses were conducted in the R statistical environment (www.r-project.org). The yearly trend in the proportion of hunter-killed cubs was analysed using a general linear model (GLM), assuming a quasibinomial distribution for the ratio of the annual number of shot cubs/older shot bears, weighted by the number of harvested older bears. Temporal autocorrelation (ACF) did not exist (the 1st- and 2nd-order autocorrelations were < 0.2). The Durbin–Watson statistic for the 1st order autocorrelation was 1.568, with a p-value of 0.095.

To test the spatial distributions of hunter-killed cubs and yearlings, we constructed a binomial (Bernoulli) model where the response variable in the model was the event that the dead bear was a cub (coded as 1, otherwise 0). The explanatory variables in the final model were the sex of the bear, distance from the Russian border and their interaction. The interaction term revealed a possible difference in the killing probability between female and male cubs in relation to the distance from the Russian border. The x- and y-coordinates (EUREF) of the locations of the dead bears were used in the model to reduce the effect of possible spatial autocorrelation. For comparison, we also generated the same models for the legally harvested yearlings.

Model construction and expression

The Akaike information criterion (Burnham and Anderson 2002) could not be used for model construction because the model was computed using the quasi-likelihood algorithm. The variable year was used in the final model as a random effect because the dead bears were nested within

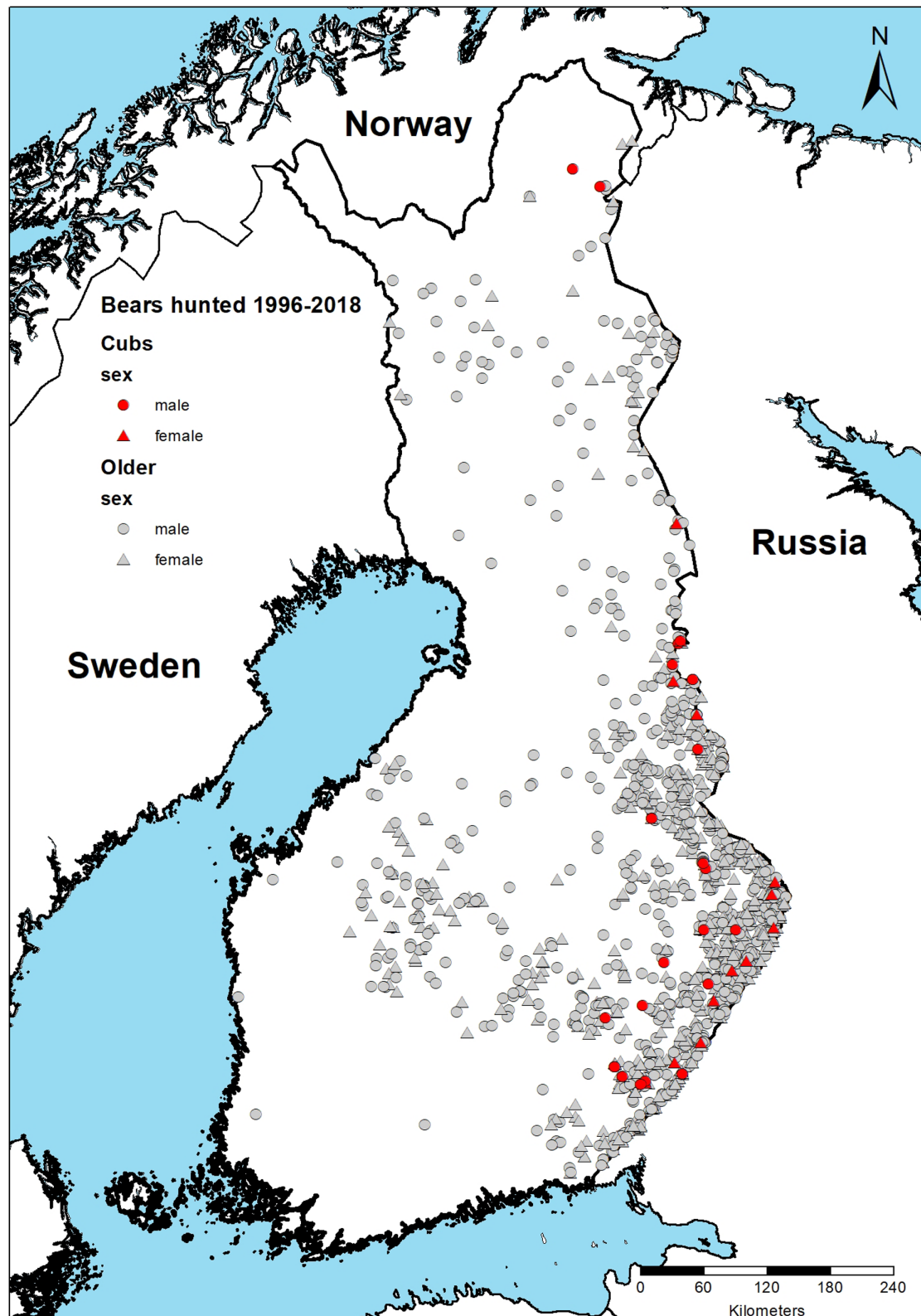


Figure 1. Bears of known age harvested by hunters in Finland 1996–2018.

the years. As a result of doing so, the exponential spatial correlation structure used was meaningful. The spatial correlation structure considered that if a dead bear (killed in a certain year) was a cub, it is more likely that another hunter-killed dead cub would be found near the first one. Thus, the

year (23 years) as a random factor was treated as ‘a random block’ that included the dead bears with their spatial coordinates. In addition, the year and its interaction with bear sex were tested as a fixed covariate (continuous variable) to observe the possible trends. The interaction of year and sex

suggested that there were no statistically significant (at the 5% risk level) differences between the coefficients for female and male cubs ($t_{1434} = 0.80$, $p = 0.43$). Furthermore, the significance of the main effect of covariate year was nonsignificant ($t_{21} = -1.37$, $p = 0.17$). Thus, the final model was built without the fixed covariate year.

The mixed effects model considering the spatial autocorrelation was computed using the R function `glmmPQL` in the R package MASS (Venables and Ripley 2002). The function only allows the use of one correlation structure for the residuals (R-matrix).

The logistic mixed model with a spatial autocorrelation term can be described as follows (Eq. 1):

$$y_{ij} \sim \text{binomial}(n_{ij}, p_{ij})$$

$$\text{logit}(\pi_{ij}) = \ln\left(\frac{\pi_{ij}}{1 - \pi_{ij}}\right) = f(X_{ij}, \beta) + \mu_i + pA_{ij} + \mu_{ij}$$

where y is the probability of the event, i.e. ‘dead bear is a cub’. Binomial (n , p) denotes the binomial distribution with parameters (n describes the binomial sample size, in our case the total number of hunter-killed bears, and p describes the proportion or probability of the occurrence

of dead cubs). Here, $\ln\left(\frac{\pi_{ij}}{1 - \pi_{ij}}\right)$ is a logit-link function,

and $f(\cdot)$ describes the linear function with arguments X_{ij} (i.e. fixed predictors) and β (i.e. fixed parameters). The term μ_i represents random year effects (the observations of dead bears nested within the years), and pA_{ij} describes the estimated coefficient of the spatial autocorrelation of the residuals at the lowest level (estimated range in Table 1). The spatial autocorrelation was weak, but it was estimated for theoretical reasons. The spatial autocorrelation of the residuals was also assessed using correlograms. The R package `ncf` (Bjornstad 2020) and its function `spline.correlog` were used to define the spatial correlation.

The dispersion (e.g. over-dispersion, cf. Browne et al 2005) in the logistic model was estimated and expressed as the term μ_{ij} . If there was no over- (or under-) dispersion, the value of the term (variance) should be 1 (expressed as the residual in R function `glmmPQL`).

Results

The annual proportion of cubs among bear killed by hunters showed a weak, nonsignificant decreasing trend during our study period (Fig. 2, general linear model, $t_{22} = -1.864$, $p = 0.076$). The sex ratio among inadvertently shot cubs was male biased (67%; 26 males, 13 females) compared to an equal distribution ($\chi^2_1 = 4.333$, $p = 0.037$). Among the hunter-killed yearlings, the male bias was also significant (59% males, $n = 228$, $\chi^2_1 = 7.74$, $p = 0.005$).

The proportion of cubs among bear killed by hunters was not related to the distance from the Russian border (Table 1), but a significant sex-by-distance interaction suggested that female cubs were killed relatively more often near the Russian border (Table 1, Fig. 3). Among the yearlings, the sex of the harvested bear was not related to the distance from the Russian border (Table 1, Fig. 3).

Discussion

Inadvertent shooting of brown bear cubs seems to be above all an ethics problem in Finland. We suggest that influences on the Finnish bear population are marginal due to the low number of deaths and the male bias in the hunter-killed cubs. Hence, based on demographic parameters in the Scandinavian brown bear population (Steyaert et al. 2012), the proportion of cubs in Scandinavia can be assumed to be approximately 25% in spring (Jon E. Swenson, pers. comm. 2020). Using this estimate and the proportion of cubs in Finnish hunting bags (2.7%), we can infer that the hunter kill rate of cubs relative to the hunter kill rate of older bears is $2.7\%/0.25 - 97.3\%/0.75$, i.e. $0.108 - 1.297 = 8.3\%$ due to inadvertent shooting during their first season of life. In

Table 1. Parameter estimates and t-tests for the logistic model predicting that a dead bear is a cub or the dead bear is a yearling. The χ^2 test was used for the analysis of deviance, and the t-test was used for the test of the estimated coefficients. SE denotes the standard error of the estimate, df denotes the degrees of freedom and p denotes the significance (probability) of the test.

Variable	Estimate	SE	df	t-value	p
Model for cubs, ROC marginal=0.61, ROC conditional=0.70					
Intercept	-3.393	0.241	1435	-14.092	< 0.001
Female sex (ref. male)	0.806	0.443	1435	1.820	0.069
Distance from Russian border (km)	-5.421e-3	3.891e-3	1435	-1.393	0.164
Sex x distance from Russian border (km)	-0.073	0.032	1435	-2.251	0.025
Random effect of year (var.)	0.090				
Range of exponential spatial correlation	19.568				
Residual (variance, expressing dispersion)	0.836				
Model for yearlings, ROC marginal=0.53, ROC conditional=0.52					
Intercept	-1.770	0.128	1435	-13.797	< 0.001
Female sex (ref. male)	0.124	0.177	1435	0.700	0.484
Distance from Russian border (km)	-0.356e-3	1.274e-3	1435	-0.280	0.780
Sex x distance from Russian border (km)	1.852e-3	1.913e-3	1435	0.968	0.333
Random effect of year (var.)	0.076				
Range of exponential spatial correlation	10.251				
Residual (variance, expressing dispersion)	0.972				

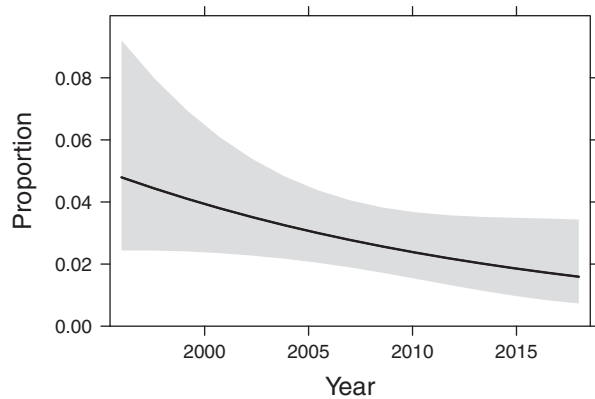


Figure 2. The annual trend (with 95% confidence zones) in the proportion of inadvertently shot cubs among all hunted bears in Finland, 1996–2018. General linear model, $t_{22} = -1.864$, $p = 0.076$.

other words, a cub's risk of being killed during the hunting season is approximately 8% of the risk of an older bear. As the mortality rate of adult bears due to hunting in Finland is not known, we cannot estimate the annual mortality rate

for cubs. However, it is unlikely to exceed 1% per year based on the aforementioned estimate. This figure might, however, be a slight underestimate because hunting bags indicate a more male-biased bear population and, consequently, a lower proportion of cubs in Finland than in Scandinavia (Bischof et al. 2008, Kojola et al. 2020). In addition, some cub deaths might be hidden, as the penalty usually includes a considerable fine, the confiscation of the hunting weapon and the loss of hunting rights for a certain number of years. Furthermore, there may be a social barrier to hunters reporting having shot cubs by mistake.

Sexual size dimorphism is a possible explanation for the male bias among cubs killed by hunters during the autumn hunting season. We do not have reliable measurements of cub body size. In Sweden, the head circumference and body mass in yearling brown bears in spring were greater in males than in females (Dahle et al. 2003). Because bears do not grow during their winter sleep, it is likely that such a difference persists in autumn.

Mortality in male bear cubs can be higher than that in female cubs even without sex-dependent harvest-associated risk. Such a difference has been found in the American black

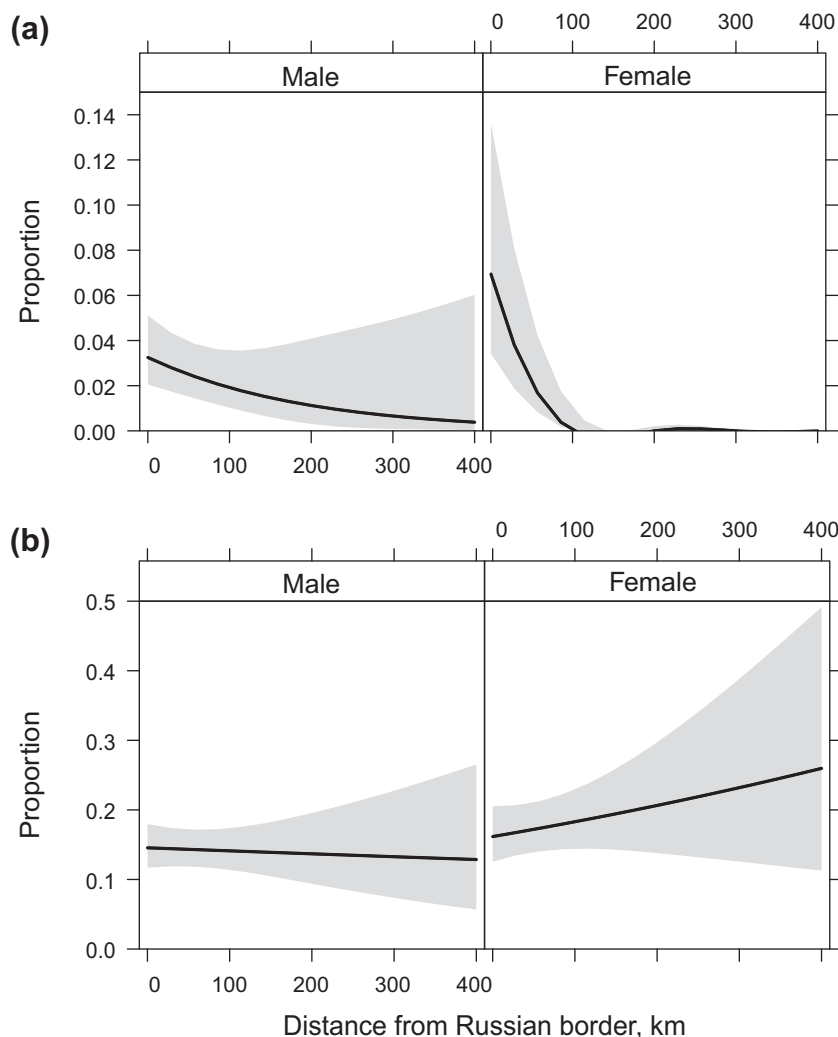


Figure 3. Relationships (with 95% confidence zones) between the distance from the Russian border and the killing of male and female cubs by hunters (a) and the killing of male and female yearlings by hunters (b) in Finland 1996–2018. Generalized linear models (Table 1).

bear, *Ursus americanus* (Elowe and Dodge 1989). This differential mortality was difficult to explain by 'natural reasons' alone because there was no evidence that male and female black bear cubs did not remain equally in the company of the mother (Elowe and Dodge 1989). The risk of being killed by a hunter is greater among male cubs than female cubs, which might be due to their larger body size. This greater body size might increase the risk of death due to hunting because yearlings can be legally harvested by hunters, and male cubs may approach the size of small yearlings. In some mammals, spatial behaviour may differ between female and male offspring, such that males move farther away from their mother than females (Guinness et al. 1979, King et al. 2015). However, before the age of weaning, distance to the mother may be independent of the sex of the offspring (Alley et al. 1995, French 1998). For brown bears, we did not find evidence in the literature indicating differences between male and female cubs in relation to the distance from the mother.

The yearly trend in the proportion of hunter-killed cubs exhibited a nearly significant decrease. If this (non-significant) correlation represent a factual trend, it may possibly be due to implementation of educational programs by hunter organizations, albeit systematic education is still lacking. A compulsory short course about the differentiation of cubs from yearlings linked to a shooting exam could be a solution to reduce the rate of inadvertent killings of cubs further. In the imminent vicinity of the Russian border, however, the number of deaths may be less influenced by educational programs because, the killing of those cubs is more likely to be intentional, motivated by a risk of losing a dog.

Our results did support the idea that greater experience among hunters decreases the risk of a cub being killed inadvertently. The risk was proportionate near the Russian border, where hunting has been practised for more years than in regions farther from the border.

Spatial patterns in the sex ratio existed in inadvertently killed cubs but not in legally shot yearlings. The reduction in the probability of killing female cubs as the distance from the eastern border increases may be related to Finnish bear harvest management and hunting practices. Most bears from the quotas reserved for the eastern provinces are shot at the eastern border (Fig. 1), usually within a few weeks after the beginning of the hunting season. This situation may intensify competition among hunters and make them less careful. Another reason may be related to Finnish bear hunting practices. Almost all bears in Finland are hunted using bear-hunting dogs (Servheen et al. 1999, Luke unpubl. statistics), and a good bear-hunting dog is 'priceless' to a hunter, often requiring years of training. The border can be passed only via a few frontier stations, and a valid visa is required for passage. Dogs are usually equipped with global positioning system (GPS) transmitters to which the hunter has online connections via a global mobile system (GSM). In a situation in which it is obvious that the dog will follow the bear into Russia, hunters may become less selective regarding the size of the young bear to prevent the loss of the dog. Unleashed hunting dogs that follow mobile game, such as bears, may drift tens of kilometres east from the border, which may ultimately result in their permanent loss.

The full protection of family groups is probably the most efficient method of decreasing the inadvertent shooting of cubs. In Sweden, all family groups with dependent cubs are protected from hunting, and extremely few cubs have been killed by hunters. However, the total harvest was slightly greater than that in Finland (only 9 cases in 1993–2015, data on 1608 reproductive events, Van de Walle et al. 2018). The full legal protection of all family groups could be ethically more convenient. However, in hunted populations, the ban can affect population demographics by prolonging mother–offspring bonds (Bischof et al. 2018, Van de Walle et al. 2018).

Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.3xsj3txgf>> (Kojola et al. 2021).

References

- Ahti, T. et al. 1968. Vegetation zones and their actions in north-western Europe. – *Ann. Bot. Fenn.* 5: 169–211.
- Alley, J. C. et al. 1995. Mother–offspring interactions in feral goats – a behavioural perspective to maternal investment. – *N. Zeal. J. Zool.* 22: 17–23.
- Bischof, R. et al. 2008. Hunting patterns, ban on baiting and harvest demographics of brown bears in Sweden. – *J. Wildl. Manage.* 72: 79–88.
- Bischof, R. et al. 2018. Regulated hunting re-shapes the life history of brown bears. – *Nat. Ecol. Evol.* 2: 116–123.
- Bjornstad, O. N. 2020. ncf: spatial covariance functions. – R package ver. 1.2-9. <<https://CRAN.R-project.org/package=ncf>>.
- Bragina, E. V. et al. 2015. Rapid declines of large mammal populations after the collapse of the Soviet Union. – *Conserv. Biol.* 29: 844–853.
- Browne, C. et al. 2005. Variance partitioning in multilevel logistic models that exhibit overdispersion. – *R. Stat. Soc.* 168: 599–613.
- Bunnell, F. L. and Tait, D. E. N. 1985. Mortality rates of North American bears. – *Arctic* 38: 316–323.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and inference: a practical information–theoretic approach, 2nd edn. – Springer.
- Dahle, B. and Swenson, J. E. 2003. Factors influencing length of maternal care in brown bears *Ursus arctos* and its effect on offspring. – *Behav. Ecol. Sociobiol.* 54: 352–358.
- Dahle, B. et al. 2003. Correlates with body size and mass in yearling brown bears *Ursus arctos*. – *J. Zool.* 269: 273–283.
- Elowe, K. D. and Dodge, W. E. 1989. Factors affecting black bear reproductive success and cub survival. – *J. Wildl. Manage.* 53: 962–968.
- French, J. M. 1998. Mother–offspring relationships in donkeys. – *Appl. Anim. Behav. Sci.* 60: 253–258.
- Guinness, F. A. et al. 1979. Mother–offspring association in red deer (*Cervus elaphus* L.) on Rhum. – *Anim. Behav.* 27: 536–544.
- Hagen, S. et al. 2015. Evidence of rapid change in genetic structure and diversity during range expansion in a recovering large terrestrial carnivore. – *Proc. R. Soc. B* 282: 20150092.
- Heikkinen, S. et al. 2020. Karhukanta Suomessa 2019. (In Finnish: Brown bear population in Finland 2019) – Luonnonvara- ja biotalouden tutkimus 26/2020. – Luonnonvarakeskus, Helsinki.

- Hrdy, S. B. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. – *Ethol. Sociobiol.* 1: 13–40.
- Huber, D. et al. 2008. A multidimensional approach to managing the European brown bear in Croatia. – *Ursus* 19: 22–32.
- King, W. J. et al. 2015. Mother–offspring distances reflect sex differences in fine-scale genetic structure of eastern grey kangaroos. – *Ecol. Evol.* 5: 2084–2094.
- Kojola, I. and Heikkinen, S. 2006. Structure of expanded brown bear population at the edge of range in Finland. – *Ann. Zool. Fenn.* 43: 258–262.
- Kojola, I. et al. 2020. Has the sex-specific structure in Finnish brown bear population changed during 21 years? – *Wildl. Biol.* 2020: wlb.00575.
- Kojola, I. et al. 2021. Data from: Inadvertent shooting of brown bear cubs in Finland: what can managers do to reduce it? – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.3xsj3txgf>>.
- Kopatz, A. et al. 2019. Estimation of gene flow into the Scandinavian brown bear population. – NINA Report 1618, 27 p.
- Krofel, M. et al. 2012. Demography and mortality patterns of removed brown bears in a heavily exploited population. – *Ursus* 23: 91–103.
- LeCount, A. L. 1987. Causes of black bear cub mortality. – *Int. Conf. Bear Res. Manage.* 7: 75–82.
- Ordiz, A. et al. 2008. Distance-dependent effect of the nearest neighbor: spatiotemporal patterns in brown bear reproduction. – *Ecology* 89: 3327–3335.
- Pulliainen E. 1990. Recolonization of Finland by brown bear in the 1970s and 1980s – *Aquilo Ser. Zool.* 27: 21–25.
- Servheen C. et al. 1999. Bears. Status survey and conservation action plan. IUCN/SSC Bear Specialist Group. – IUCN Publication Unit, Cambridge, UK.
- Steyaert, S. et al. 2012. The mating system of the brown bear. – *Mammal Rev.* 42: 12–34.
- Støen, O.-G. et al. 2006. Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. – *Oecologia* 148: 356–364.
- Swenson, J. E. and Sandegren, F. 1996. Sustainable brown bear harvest in Sweden estimated from hunter-provided information. – *J. Wildl. Res.* 1: 229–232.
- Swenson, J. E. et al. 2001. Factors associating with loss of brown bear cubs in Sweden. – *Ursus* 12: 69–80.
- Swenson, J. E. et al. 2017. Challenges of managing a European brown bear population; lessons from Sweden, 1943–2013. – *Wildl. Biol.* 2017: wlb.00251.
- Van de Walle, J. et al. 2018. Hunting regulations favors slow life histories in a large carnivore. – *Nat. Commun.* 9: 1100.
- Venables W. and Ripley B. 2002. Modern applied statistics with S, 4th edn. – Springer.