February 2012

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Adaptive Management of the Brown Bear Population in Hokkaido, Japan

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ABSTRACT

In Hokkaido, Japan, recent trends concerning the intrusions of the brown bear (*Ursus arctos*) into crop fields and a subsequent increase in agricultural damage have highlighted the need for new and more effective population management strategies. To devise such strategies, we focused on a well-defined, previously studied brown bear population living in the Oshima Peninsula region of Hokkaido, and constructed a population dynamics model for adult females. The model construction was based on the ecological and physiological characteristics of the Oshima Peninsula population, with particular emphasis on bear behavior (levels of aggressiveness and intrusiveness) and human-bear interactions (bear kills, food conditioning, and aversive conditioning). To predict the future population dynamics, we ran stochastic simulations over a period of 100 years. We used the simulation outputs to estimate the risk of management failure under four plausible scenarios, including the scenario that represents the present management practices. The results of the analysis indicated that the present management practices could not satisfactorily resolve the problem of increasing agricultural damage. However, an adaptive management strategy successfully reduced the risk of management failure to a negligible level.

Keywords: ecological risk, population dynamics model, food conditioning, aversive conditioning, human-bear conflict, nuisance bear

1. Introduction

In Hokkaido, Japan, potentially alarming trends in the interaction between brown bear (*Ursus arctos*) and local residents call for innovative and more effective population management strategies. While the brown bear population in question has historically been known to cause agricultural damage and injuries, in the period from 1988 through 2005, a 6.7 % annual increase rate in the planned bear kills was accompanied by more than a 5 % annual increase rate in the amount of agricultural damage (Mano, 2009). These trends may result in social pressure for more aggressive bear kills, which in turn may harm the viability of the brown bear population, especially because the causes behind the rising tendency toward crop field intrusions are poorly understood. In this context, the introduction of new and non-lethal techniques, such as aversive conditioning with relocation, may provide a new layer of flexibility for management of the brown bear population, improving the chances of its survival and suppressing the number of crop field intrusions below the socially acceptable level.

A quick and cost-effective manner to test the consequences of introducing new management methods is the modeling approach. In Hokkaido, for example, modeling was used to examine a management policy for sika deer (Matsuda et al., 1999). In the case of the brown bear, modeling was applied to produce concrete conservation management recommendations in Slovenia (Jerina et al., 2003). In the central Apennines, Italy, habitat modeling proved to be useful in identifying critical areas for a brown bear conservation strategy (Posillico et al., 2004). In the present study, we focus on examining the effectiveness of combining existing lethal (i.e. planned bear kills) and new non-lethal (i.e. aversive conditioning with relocation) population management methods in an adaptive manner. For that purpose, a population dynamics model is formulated together with several realistic management scenarios. The model is run to make future projections of the population size and estimate risks of management failure under each scenario. We assume that the failure occurs if either of the two management goals is not satisfied; (i) the number of intrusions into crop fields is not suppressed below the acceptable level, or (ii) a viable population is not maintained at all times. Because the lethal method is in direct conflict with the goal of maintaining a viable population, while aversive conditioning may be unsuccessful in suppressing bear intrusions (Mazur, 2010; Nakanishi et al. 2007), a tradeoff between the two management goals is a fundamental property of all scenarios considered. The risk of failure is a quantitative measure of our ability to balance this tradeoff, and therefore provides an objective criterion for assessing the relative performance of the scenarios to be evaluated. Moreover, the modeling approach enables us to perform such an evaluation long before the time consuming and costly implementation of any management policy takes place.

2. Study area

To simplify the analysis performed henceforth, we restrict its scope to a geographically narrow area.

In Hokkaido, the existence of the three distinct brown bear subpopulations allows for such a restriction (Matsuhashi et al., 1999). Particularly interesting in this context is the southwestern subpopulation residing on the Oshima Peninsula, partly because it is isolated from the other two subpopulations, and partly because it is receiving considerable scientific attention with respect to the increasing occurrence of bear intrusions (Mano, 2009; Tsuruga and Mano, 2008). The Oshima Peninsula – an area of 7,300 square kilometers and a home to around 500,000 inhabitants – hosts a brown bear population of 800 ± 400 individuals (Hokkaido prefectural government, 2010), characterized by (i) no significant changes in the bear density index for almost two decades, (ii) a 5.8 % annual increase rate in the number of bear kills, and (iii) the highest incidence of bear-inflicted agricultural damage during the late summer. These findings suggest that although the population size appears stable, the number of bears killed for intruding into crop fields continues to increase. The late summer is an especially problematic season. During this period, the diet of the bears shifts from early summer foods to autumn foods, i.e. from herbaceous plants and ants to berries, acorns, and nuts (Sato et al., 2005). On the Oshima Peninsula, which is approximately 80 % covered by woodland, acorns and nuts originate from the predominant species like the Mongolian oak (*Quercus crispula*) and Japanese beech (*Fagus crenata*). At times, the shift from early summer foods to autumn foods does not proceed smoothly because acorns and nuts are still unripe when the herbaceous plants die above ground and are no longer suitable as foodstuffs. Consequently, during this period the bears may rely heavily on crops to survive. Once a bear learns a particular foraging behavior and becomes food conditioned (Gunther and Wyman 2008), it is probable that the acquired knowledge will be quite persistent (Mazur, 2010) and subject to vertical transfer from sows to cubs (Mazur and Seher, 2008), potentially aggravating the problem of bear intrusions.

3. Materials and methods

3.1. Model development

We constructed a population dynamics model for adult female brown bears on Oshima Peninsula by considering their essential ecological and physiological characteristics (e.g. feeding habits, reproductive output, and density effects). The reason for turning our attention to adult female bears originated from a principle that adult female survival is crucial to the well-being of populations of the long lived vertebrates and possibly many other sexually reproducing species (Eberhardt, 2002). As an illustration of this principle, it was found that the population growth rate of black bear (*Ursus americanus*) in the Bow Valley of Banff National Park, Alberta, was most sensitive to changes in adult female survival (Hebblewhite et al., 2003).

One might express a concern that the number of male bears should be tracked at least in the context of crop field intrusions – Tsuruga and Mano (2008) indeed found a bias toward males (64.5 % of the total) in catch data from Oshima Peninsula. Whereas a larger home range of male brown bears (Dahle and Swenson, 2003) may have been a contributing factor to the observed bias, males appear to be far more reckless when entering a new area, and therefore tend to get caught more easily than females. Another reason not to attach too much of an importance to the observed bias is the previously mentioned vertical transfer of food conditioning from sows to cubs meaning that, unless feeding habits change significantly in the adult stage, the nuisance behavior should be rather equally distributed between sexes.

In addition to considering adult female bears, our objective of identifying effective management strategies that can ensure the long-term coexistence of human residents and brown bears in the same geographical area, focused us on bear behavior (levels of aggressiveness and intrusiveness) and human-bear interactions (culling, food conditioning, and aversive conditioning). During the model construction, the following assumptions were made:

Assumption 1: We consider the non-nuisance and nuisance female bears to be distinguishable based on their behavior. How clearly this distinction can be drawn is reflected in the language of the indigenous Ainu people, who call non-nuisance bears "kim-un-kamuy" or "god in the mountain" and nuisance bears "wen-kamuy" or "bad god". Rigorous criteria for discriminating between these two bear types (Table 1) are described in the literature (Mano, 2009; Tsuruga and Mano, 2008). For modeling purposes, we assume that non-nuisance bears either evade or ignore human presence and do not cause any agricultural damage (phases 0 and 1 in Table 1). In contrast, nuisance bears are aggressive toward humans or tend to invade crop fields (phases 2 and 3 in Table 1). We also assume that during a single year, a fraction *m* of non-nuisance bears adopt new foraging behavior, become food conditioned, and effectively turn into nuisance bears. Henceforward, $N_0(t)$ denotes the number of female nuisance bears in year *t*, whereas $N_1(t)$ denotes the number of non-nuisance females in the same year. The female population size in year *t* is $N(t) = N_0(t) + N_1(t)$. The year counter *t* runs from 0 to 123, corresponding to the time period between 1987 and 2110. The past 23 years, from1987 to 2009, serve as a run-up period to reduce the influence of the initial values, and to provide output for a convenient comparison with existing data. The future predictions span a 100 years period from 2010 to 2110.

Assumption 2: The level of catch effort is controllable by the bear managers and varies over time to counteract unwanted bear behavior. For nuisance bears, the manager can vary the level of effort by adjusting the catch rate $\gamma(t)$. We can interpret the value of the catch rate as the probability of catching a single nuisance bear during a period of one year. Because the distinction between nuisance and non-nuisance bears is not absolute, the manager may catch a non-nuisance bear by mistake. The catch rate in this case is $F\gamma(t)$, where F is the false-catch coefficient.

Assumption 3: The degree of reliance on aversive conditioning is also controllable by the manager and varies over time to counteract unwanted bear behavior. The release rate, $\alpha(t)$, indicates the fraction of bears caught in one year that are subjected to aversive conditioning and released again into nature by the manager. As the effectiveness of aversive conditioning cannot be guaranteed (Mazur, 2010), only a fraction β of the nuisance bears subjected to aversive conditioning will abandon their unwanted behavior and become successfully reformed. A fraction $1-\alpha(t)$ of caught bears is eventually culled.

Assumption 4: The survival rates S of both nuisance and non-nuisance bears are assumed to be equal. A comprehensive study of adult females of the long-lived vertebrates suggests a sequence of changes in vital rates taking place when a population faces the scarcity of resources (Eberhardt, 2002). In this sequence, the last vital rate to change (that is, decrease) is survival, indicating its relative stability under all except the harshest of conditions. As an illustrative example, we note that the exposure of brown bears to crude oil had little effect on the survival of female adults on the coast of Katmai National Park, Alaska (Sellers and Miller, 1999).

Assumption 5: The seed output of masting trees may exert various effects on bear populations (Mattson et al., 1992; Rogers, 1976). Here we assume that the catch following intrusions into crop fields is more probable if the average acorn production is low and vice versa. For example, the data on the Asiatic black bear (*Ursus thibetanus*) in the Tohoku region of Japan show a negative correlation between the number of nuisance bears killed and beech seed output (Oka et al., 2004). In Furano, central Hokkaido, existing evidence suggests that brown bears use crops as an alternative food source to acorns of *Quercus* spp. from September through November (Sato and

Endo, 2006). A stronger tendency toward intrusions implies that the catch will increase even if the effort is constant, which is why we defined acorn production-dependent catch probabilities of nuisance bear and non-nuisance bears in year t using relationships $p_0(t)=\gamma(t)\exp[-A(t)]$ and $p_1(t)=F\gamma(t)\exp[-A(t)]$, respectively. To appropriately include the effects of acorn production, $A(t)$, into the model, we estimated the seed output autocorrelation function for Mongolian oak at Ogawa Forest Reserve in Ibaraki Prefecture from a 10-year dataset (1995-2004) obtained from the Forestry and Forest Products Research Institute (T. Masaki, personal communication). A strong negative correlation with a two-year lag suggested that we should use a stationary random process with a zero mean

$A(t+2)=\rho A(t)+\varepsilon(t)$, (1)

where ρ is the autocorrelation coefficient. The random term $|\varepsilon(t)|\leq 1+\rho$ is drawn from the uniform distribution. $A(t)$ ranges between -1 and 1.

Assumption 6: The observed age of first parturition of the brown bear females on Oshima Peninsula is four years, but reproductive success is markedly higher among females six years old or older (Mano and Tsubota, 2002). To implicitly represent the role of the juvenile stage in the model, we assume that the number of adult females in year $t-5$ determines the number of juveniles becoming reproductively active in year $t+1$, where the parameter connecting these two numbers is the average recruitment rate R. In view of experimental evidence suggesting considerable density effects (Czetwertynski et al., 2008), especially in the case of adult females, the average recruitment rate R is allowed to operate only in the limit of a negligibly small population. To include density effects in the model, we use the expression $R\exp[-\omega N(t-5)]$, where ω is the strength of the density effects. For an alternative interpretation of this parameter, note that the carrying capacity K

is linked to ω, R and S by $K\omega = \log\left(R/(1-S)\right)$. In addition, recruitment depends on acorn production during the autumn of year $t-6$, denoted $A(t\text{-}6)$, because the reproductive rate decreases as a consequence of food shortage (Mano and Tsubota, 2002; Rogers, 1976). The resulting expression for the recruitment rate $r(t)$, with the strength of the density effect included, is $r(t) = R\exp\left[\left(A(t-6)-1\right)\omega N(t-5)\right]$.

While the survival rate of adult females of the long-lived vertebrates may be relatively stable in conditions of scarce resources, the same appears not to be the case for the reproductive rate (Eberhardt, 2002). Investigations performed on black bears seem to confirm this notion (Rogers, 1976). As a result, assuming the same recruitment rate for non-nuisance and nuisance bears (our default setting in model simulations) may not be the most realistic modeling assumption – nuisance bears should, after all, be more adept in finding food when acorn production fails. Facing a lack of information on differences between the recruitment rate of non-nuisance and nuisance bears on the Oshima Peninsula, we exploit the strength of the modeling approach and test instances of 20 % lower recruitment rate for non-nuisance bears in comparison to the default setting.

Based on assumptions 1 through 6, conveniently summarized in Figure 1, the equations for the population dynamics are

$$N_0(t+1) = SN_0(t) + r(t)N_0(t-5) - \alpha(t)\beta C_0(t) + mN_1(t) - [1-\alpha(t)]C_0(t), \quad (2a)$$

$$N_1(t+1) = SN_1(t) + r(t)N_1(t-5) + \alpha(t)\beta C_0(t) - mN_1(t) - [1-\alpha(t)]C_1(t), \quad (2b)$$

where the first two terms on the right-hand side of both equations represent the number of surviving bears from year t to $t+1$ and the number of juveniles in year $t-5$ entering adulthood in year $t+1$. The third term in equations (2a) and (2b) counts the number of nuisance bears successfully reformed by aversive conditioning. Similarly, the fourth term in equation (2a) includes the number of newly food-conditioned nuisance bears. This number must then be deducted from the number of non-nuisance bears in equation (2b). Finally, the last term represents the number of bear kills. The random variables $C_i(t), i = 0,1$, representing catch numbers, are taken from a binomial distribution with parameters $N_i(t)$ and $p_i(t), i = 0,1$. If we denote the cumulative distribution function for binomially distributed random variable as

$$F_i(x; N_i, p_i) = \Pr[C_i \leq x] = \sum_{j=0}^{\lfloor x \rfloor} \binom{N_i}{j} p_i(t)^j (1 - p_i(t))^{N_i - j}, \quad (3)$$

where $0 \leq x \leq N_i$ and $\lfloor x \rfloor$ is the greatest integer less than or equal to *x*, then catch numbers are given by $C_i(t) = F_i^{-1}(y; N_i, p_i(t)), i = 0,1$, with $0 \leq y \leq 1$ being a random number drawn from the uniform distribution.

3.2. Parameter Estimation

The parameter values (Table 2) appearing in the model of female brown bear population dynamics described above were extracted from the literature to the maximum extent possible. For the average recruitment rate *R*, we relied on the known reproductive characteristics of the brown bears on Oshima Peninsula, where the mean litter size was 1.8 cubs and the interval between births was 2.3 to 3 years (Mano and Tsubota, 2002). We assumed a sex ratio of 0.5. The survival rates for grizzly bears in Banff National Park, Alberta, were 0.71 for cubs of the year, 0.91 for yearlings, and 0.72 for the remaining four years to maturity (Garshelis et al., 2005). Quite similar mean litter sizes and survival rates were reported for many European brown bear populations (Jerina et al., 2003; Frkovic et al., 2001). From these data, we estimated the average recruitment rate to be $0.5 \times 1.8 / 2.5 \times 0.71 \times 0.91 \times 0.72 = 0.17$. In the case of adult females, the natural survival rates of the long-lived vertebrates were found likely to exceed 0.95 (Eberhardt, 2002). Since the observed survival rate of various bear populations confirmed this notion (Garshelis et al., 2005; Sellers and Miller, 1999; Wielgus and Bunnell, 1994), we set $S = 0.95$.

The release rate α, as stated in assumption 3 above, is a parameter controllable by population managers, and therefore could not be assigned a single value. For the Asiatic black bear in the western Chugoku Mountains, Japan, release rates from 1996 to 2006 ranged between a minimum of 0 and a maximum of 0.8 (Kanamori et al., 2008). The same range was used in our simulations. A related parameter to which also a single value could not be assigned is the success rate of aversive conditioning β. Field observations suggested that the value of this parameter depends on the promptness in delivering aversive conditioning, a method used to do so, and the age of the targeted bear (Mazur, 2010), all of which are sources of considerable uncertainty. To make the model results realistic, but conservative, we took the success rate of 60 % recorded in the case of Asiatic black bear in Hyogo Prefecture (Yokoyama et al., 2008) as the maximum for our range of possible values. The minimum success rate was set to 30 %. One value was drawn randomly from the selected range prior to each simulation run.

To estimate realistic values for the remaining four parameters (the false-catch coefficient F, the change rate from a non-nuisance bear to a nuisance bear m, the catch rate γ, and the carrying capacity K), we relied on the information presented in Figure 2. Beginning from the catch statistics of brown bears on Oshima Peninsula between 1987 and 2009 (Hokkaido prefectural government, 2010), we estimated the past size of the female population with a well-documented, harvest-based method (Matsuda et al., 2002). We also assumed that the number of nuisance bears between 2001 and 2003 was known from the results of surveys conducted on Oshima Peninsula (Tsuruga and Mano, 2008). We then limited the range of possible parameter values with the following restrictions: (i) the modeled number of female brown bear individuals between 1993 and 2009 must remain within the 95 % confidence interval of the harvest-based (past) population size, while (ii) the modeled number of nuisance bears must increase from 1993 to 2009, but remain within the limits established for the period 2001-2003. With these restrictions in mind, we searched the parameter space using a numerical implementation of the maximum likelihood estimation method that has been thoroughly described in the ecological literature (Fujiwara et al., 2005). The likelihood function consisted of the probability that the simulated total catch $C(t) = C_0(t) + C_1(t)$ is equal to the actual culling data C_t in year t:

$$\begin{aligned} L(\theta | C_t) &= \Pr[C(7) = C_7; \cdots ; C(t) = C_t] \\ &= \Pr[C(t) = C_t | C(t-1) = C_{t-1}, \cdots, C(7) = C_7] \\ &\times \Pr[C(t-1) = C_{t-1} | C(t-2) = C_{t-2}, \cdots, C(7) = C_7] \\ &\times \cdots \times \Pr[C(7) = C_7] \end{aligned}, \quad (4a)$$

$$\Pr[C(t) = C_t | C(t-1) = C_{t-1}, \cdots, C(7) = C_7] = \sum_{X=0}^{C_t} \Pr[C_0(t) = X] \Pr[C_1(t) = C_t - X], \quad (4b)$$

where $C_i(t), i = 0, 1$ represent catch numbers for two types of bears determined by equation (3), and t(=7, 8, …, 23) indicates a year within the parameter estimation period from 1993 to 2009 (note that assumption 6 above precludes the model from producing meaningful predictions before 1993).

In addition to the four parameters mentioned above, the likelihood function depended on the initial (1987-1992) population size ξ relative to the harvest-based 95 % confidence interval and on the initial (1987-1992) ratio of nuisance to non-nuisance bears, i.e. N_0/N_1. We defined quantity ξ by $N(t) = \hat{N}_l(t) + \xi(t)(\hat{N}_u(t) - \hat{N}_l(t))$, where $\hat{N}_u(t)$ and $\hat{N}_l(t)$ represent the upper and lower limits of the 95 % confidence interval for the female population size obtained by the harvest-based method in year t(=1, 2, …, 6).

The search for maximum likelihood estimates over the parameter space revealed significant covariances between the change rate m (from a non-nuisance to a nuisance bear), the catch rate γ, and the false-catch coefficient F (Figure 3). Namely, if the estimated value of the change rate was relatively high (low), then the catch rate would also tend to be high (low), whereas the false-catch coefficient would tend to be low (high). To understand these covariances, we considered two opposite situations. In the case of high change rate m, food-conditioned bears are the ones predominantly intruding into crop fields and getting caught. Hence, their catch rate γ must be high, while the catch rate of non-nuisance bears $F\gamma$ must remain low. In the opposite case, i.e. when the change rate is low, a relatively small number of truly food-conditioned bears makes them hard to distinguish (lower γ), and therefore non-nuisance bears are the ones getting caught (higher $F\gamma$) after randomly wandering off into crop fields. To emphasize this point, consider that the definitions of non-nuisance and nuisance bears did not originate from genetic or physiological divergences, but rather from cognitive or operational differences.

Between the two described opposites – high m vs. low m – there was a continuum of intermediate m values, with their respective γ and F values, all of which were equally likely under the existing catch statistics. Covariances between model parameters, thus, made it impossible to discern a single maximum of the likelihood function given in equations (4a, b). As a consequence, constructing a management plan robust not only to process uncertainties, but also to parameter uncertainties, required testing different management scenarios under as many as possible highly likely parameter sets. Here we ran 1000 simulations per scenario, each with its own set of parameter values taken from the ranges specified in Table 2.

3.3. The Risk of Management Failure and Management Scenarios

The purpose of managing the brown bear population on Oshima Peninsula is to ensure its viability at all times and reduce the number of intrusions into crop fields to an acceptable level. For that purpose, we define two types of management failure risks. The risk of ecological management failure is the probability that the total female brown bear population size decreases to less than 25 % of the estimated population size in 2008 within the next 100 years. The risk of conflict management failure is the probability that the number of nuisance female brown bears exceeds the average maximum estimated number of nuisance females between 2001 and 2003 within the next 100 years.

Based on assumptions 2 and 3, which state that the catch and release rates are controllable by the bear managers, we define four management scenarios. Scenario 0 represents the base case and corresponds to the current management practices. This scenario keeps the catch rate constant, in accordance with estimates based on the Hokkaido Prefecture bear catch statistics on Oshima Peninsula from 1993 to 2009. The release rate is equal zero. Scenario 1 increases the catch rate by 100 % in comparison with the base case (2γ vs. γ) to explore how a more stringent control of the population size affects the risk of management failure. The release rate is variable, i.e. adjustable by the model, as a precaution against potentially dangerous decreases in population size. Scenario 2 attempts to evaluate the effects of a variable catch rate on management risks for a zero release rate. Finally, scenario 3 is a fully adaptive management strategy with variable catch and release rates.

In scenarios with variable catch and/or release rates, the model adjusts these rates according to the equations

$$\gamma(t+1) = \gamma(t) + \begin{cases} -0.1 & N_0(t) < W_{index} \\ 0.2 & N_0(t) \geq W_{index} \end{cases}, \text{(5a)}$$

$$\alpha(t+1) = \alpha(t) + \begin{cases} 0.2 & N(t) < N_{index} \\ -0.1 & N(t) \geq N_{index} \end{cases}, \text{(5b)}$$

where the initial values in 2009 (i.e. for $t = 23$) fall within the ranges specified in Table 1. The threshold levels for parameter variation, called W-index (W_{index}) and N-index (N_{index}), are optimized to minimize the risks of management failure (Figure 4).

4. Results

Under the constant catch rate scenario 0, which corresponds to the currently implemented management method, the model predicted a period of transient dynamics in which the average population size increased. As an important consequence, the number of newly recruited or food-conditioned nuisance bears exceeded the number of nuisance bears captured (Figure 5a), thus causing the risk of conflict management failure to exceed 90 % (Table 3). Despite the high level of uncertainty in the model predictions, which is represented by the wide 95 % confidence interval, the risk of ecological management failure was nonexistent. The current level of catch effort appeared to be too low to cause a population decline below 25 % of the estimated population size in 2008.

Doubling the catch rate under scenario 1 effectively controlled the population size. As a consequence, the number of newly recruited or food-conditioned nuisance bears was more closely balanced with the number of nuisance bears captured (Figure 5b), causing the risk of conflict management failure to decrease to 60 %. Despite the slight decrease in the average population size over the next 100 years, viability did not appear to be compromised, and the risk of ecological management failure was nonexistent. The model quickly reduced the variable release rate to zero because the population size almost never decreased below the N-index (equal to 150 individuals in this case).

Under the variable catch rate scenario 2, the average population size rapidly approached equilibrium due to the increase in catch rate (Figure 5c). Initially, we observed a brief period of transient dynamics in the form of an oscillation in the average population size until the catch rate approximately stabilized at a value determined by the W-index (equal to 25 individuals in this case). After the transition, the number of newly recruited or food-conditioned nuisance bears equilibrated with the number of nuisance bears captured, making the risk of conflict management failure nonexistent. However, the uncertainty in the population size remained high, and the risk of ecological management failure reached almost 40 %.

Under the adaptive management scenario 3, the average population size reached equilibrium rapidly after the model adjusted the catch and release rates to the values dictated by the W- and N-indices (in this case equal to 10 and 500 individuals, respectively). In comparison to scenarios 1 and 2, the introduction of aversive conditioning led to more protective limits for varying the release rate (500 vs. 150 individuals) and catch rate (10 vs. 25 individuals). In scenario 1, for example, the declining population would have caused the increase of the release rate only after the population size had fallen below 150 adult females. In scenario 3, the same increase would have ensued much sooner, i.e. when the population size had fallen below 500 females. The risk of ecological management failure remained nonexistent, and the risk of conflict management failure remained below 1 %. Releasing a fraction of captured nuisance bears had a stabilizing effect on the population size without decreasing the effectiveness of conflict prevention. It is interesting to note here that decreasing the recruitment rate for non-nuisance bears by 20 % had no major effect on the risk of management failure. The adaptive management strategy appeared robust with respect to an apparently important difference in the recruitment rate between the two types of bears.

5. Discussion

In this study, we identified potentially alarming trends related to the brown bear intrusions into crop fields in Hokkaido, Japan. This situation suggested the need for more effective population management strategies. We narrowed our considerations to a well-defined, systematically studied subpopulation residing on Oshima Peninsula and constructed a population dynamics model for adult females. We based the model on ecological and physiological characteristics of the Oshima Peninsula population, paying particular attention to the bears' behavior (levels of aggressiveness and intrusiveness) and human-bear interactions (bear kills, food conditioning, and aversive conditioning). Predictions of the population dynamics 100 years into the future were made using stochastic simulations. We recognized the fundamental uncertainty in the model parameters and ensured robustness of results by running 1000 simulations, each with a different but equally likely parameter set. Finally, we used the simulation results to estimate the risk of management failure for four plausible scenarios, including a scenario that represents the present management practices.

One of the risks of management failure we considered is the conflict risk, defined rather arbitrarily from past data in hope that the socially acceptable level of crop damage would not be exceeded. Taking into account that bear intrusions are not only damaging to crops, but outright dangerous to the farmers, the problem of finding out what is socially acceptable is a comprehensive one and involves simultaneous statistical analysis of various human dimensions of wildlife. Such approaches have only recently received interest in Japan (Akiba et al., 2012), but in the future could be of great help to quantitative studies – like this one – in defining concrete numerical criteria for management decisions.

We drew several key conclusions about the brown bear population on Oshima Peninsula from the model results. The analysis of the base case, scenario 0, indicated that the present management practices were ineffective in diminishing the risk of conflict. At the current level of catch effort, the brown bear population expanded well into the foreseeable future, causing the number of nuisance bears to increase beyond the acceptable limit even at a low rate of change from a non-nuisance to a nuisance bear $(m = 0.001)$.

Doubling the level of catch effort under scenario 1 suppressed the population growth without negatively affecting the ecological risk. Under the same conditions, the conflict risk decreased significantly compared with scenario 0, suggesting that the efficient control of the population size could also regulate the number of nuisance bears. The model was, therefore, more consistent with the idea that the population growth was primarily responsible for the increasing agricultural damage, rather than the alternate possibility of nuisance bears proliferating at historically unprecedented rates.

Considering the level of catch effort to be the main method for regulating the conflict risk, we examined an adaptive strategy under scenario 2, in which the level of catch effort varied in accordance with the number of nuisance bears. This strategy proved adequate to completely suppress the conflict risk, but the ecological risk increased significantly, illustrating the fundamental tradeoff between the two management goals outlined in section 2. Balancing this tradeoff more adequately required some level of aversive conditioning with relocation. As a result, we tested a fully adaptive scenario 3, with variable catch and release rates. This strategy proved adequate to achieve both management goals with negligible risks of failure. Even an apparently important difference in recruitment rates between the two types of bears had little effect on the risk of management failure.

Considering the implementation of adaptive management scenario 3 several difficulties can be identified. First, increasing the catch rate may require catching bears that did not enter into crop fields. As a consequence, organized hunting campaigns may be necessary to achieve the planned catch number. Such actions would likely increase the overall management costs, as well as the probability of mistaking a non-nuisance bear for a nuisance bear. Second, aversive conditioning may be needed to keep the ecological risk of management failure low. This, in turn, requires potentially dangerous operations (chasing, pepper spraying, shooting with slingshots or rubber slugs, etc.), which in addition to being expensive guarantee no success (Mazur, 2010). Third, for adaptive management to be effective as predicted by the model, relatively precise information on the state of the population is required. The population size and number of nuisance bears should periodically be estimated, thus requiring accurate catch statistics, surveys and other types of research targeting brown bear physiology and ecology. As a result, overall costs of managing the population would probably increase.

We should point out that one potentially interesting nonlinearity was not implemented into the model. For example, acorn production was used synonymously to the food availability, while in reality the latter non-linearly depends on the population size (i.e. when the number of individuals is small, even poor acorn production may prove nutritionally adequate). Accounting for such a subtle distinction should have had a stabilizing effect in the limit of small population size, because sufficient food availability would have resulted in lower catch rates and higher population growth rate. Neglecting this distinction, however, did not represent an act of omission, because the center of our attention was a maximum manageable population size rather than the limit of a vanishing population, and besides we consciously erred on the safe side in the sense that the ecological risk of management failure had been somewhat overestimated.

6. Conclusions

The scenarios constructed and examined in this study focused on management methods that can be most readily implemented: planned bear kills or aversive conditioning with relocation. In the model, these management methods correspond to variations in two parameter values: the catch rate $\gamma(t)$ and the release rate $\alpha(t)$. The catch rate proved to be successful in regulating the risk of conflict management failure. Under the adaptive management scenario 3, the release rate helped reducing uncertainty in the predictions of the population size, thus diminishing the ecological risk of management failure. The apparent success, however, came at the price of a severe limit on the maximum manageable population size (approximately 500 individuals). Beyond this threshold population size, the equilibrium between the number of newly recruited or food-conditioned nuisance bears and caught or reformed nuisance bears was above the level deemed desirable.

Controlling the catch and release rates may not be the only available management methods. Several preliminary experiments conducted using electrical fences to protect the crop fields from bear intrusions, and possibly prevent the occurrence of food conditioning, have shown encouraging results (Mano, 2007). Another solution, proven effective in reducing bear damage to trees (Ziegltrum, 1994), could be supplemental feeding during the critical periods of low food availability. In mathematical terms, these types of management correspond to the control of the change rate from a non-nuisance bear to a nuisance bear (decreasing *m*), or to dampening the variability of acorn production (decreasing ρ). The lower the change rate *m*, for example, the weaker the effect of food conditioning, and consequently the manageable population size could become larger. We therefore suggest that exploring preventive measures capable of reducing the incidence of undesirable bear behavior may provide more freedom in the selection of appropriate strategies and produce better solutions to the bear population management problem in the future.

Acknowledgments

We would like to express our gratitude to Dr. T. Masaki of the Forestry and Forest Products Research Institute for providing access to the Forest Dynamics Database. We are also grateful to

Dr. T. Doko for providing practical bear management advice. This work was partly supported by the grant from the Global Environment Research Fund (S2-10) from the Japanese Ministry of the Environment and by the Global COE (E-03) grant from the Ministry of Education, Culture, Sports, Science and Technology to H.M. Scholarship (no. 080755) from the Japanese Ministry of Education, Culture, Sports, Science & Technology (MEXT) allowed M.J. to conduct this research in Japan.

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Table 1. Criteria for categorizing brown bears. Phases 0 and 1 characterize non-nuisance bears, while phases 2 and 3 characterize nuisance bears.

Behavior toward crop fields	Behavior toward humans		
	Evasive	Indifferent	Aggressive
Non-intrusive	Phase 0	Phase 1	Phase 3
Intrusive	Phase 2	Phase 2	Phase 3

Table 2. List of parameters.

Definition	Symbol	Value or range used in simulations
Average recruitment rate	R	0.17
Survival rate	S	0.95
Release rate [a]	α	0 or 0 – 0.8
Aversive conditioning success rate	β	0.3 – 0.6
Acorn production autocorrelation coefficient	ρ	-0.4
Initial (1987-1992) ratio of nuisance to non-nuisance bears	N_0/N_1	0 – 0.075
Initial population size relative to the harvest-based 95 % CI during 1987-1992	ξ	0.017 – 0.819
False-catch coefficient [b]	F	0.054 – 0.999
Change rate from non-nuisance bear to nuisance bear [b]	m	0.001 – 0.302
Catch rate [a, b]	γ	0.034 – 0.447 or 0 – 0.8
Carrying capacity	K	1099 – 1790
Strength of density effect [b]	ω	$(7-11)\times10^{-4}$

[a] Controllable parameters whose values ranged from 0 – 0.8 in adaptive scenarios.

[b] Maximum likelihood estimates based on the Hokkaido Prefecture bear catch statistics on Oshima Peninsula from 1993 to 2009.

Table 3. Overview of scenarios with risks of management failure (%).

Scenarios	0	1	2	3
Release rate	0	variable	0	variable
Catch rate	constant	constant	variable	variable
Ecological risk	0	0	38.8	0.1
Conflict risk	93.4	60.2	0	0.3