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Authors: Parker, Howard, Nummi, Petri, Hartman, Göran, and Rosell, Frank

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Review article

Invasive North American beaver *Castor canadensis* in Eurasia: a review of potential consequences and a strategy for eradication

Howard Parker, Petri Nummi, Göran Hartman & Frank Rosell

Seven North American beavers *Castor canadensis* (Cc) were introduced into Finland in 1937 to supplement an ongoing reintroduction of the nearly extinct Eurasian beaver *C. fiber* (Cf). At that time, many zoologists recognised only one species. However, in 1973, chromosome counts (Cf = 48, Cc = 40) acknowledged two species, and Cc became an invasive alien. Recently, expanding populations of both species have converged on two fronts in Finland and northwestern Russia. According to Gause's competitive exclusion principle, two species with identical niches cannot coexist indefinitely . The imminent question is whether coexistence or competitive exclusion will ultimately result, with the possible regional extirpation or eventual extinction of Cf. We reviewed published cases of interspecies contact and compared their life history, ecology and behaviour. The few published incidences of contact were inconclusive with respect to competitive advantage. Body size is similar, but Cc litter size is slightly greater. Only minor differences in life history, ecology and behaviour were found to exist, suggesting nearly complete niche overlap. Though competitive exclusion resulting in the extinction of a native mammal by an alien congener at the continental landscape scale has been rare, the process may be difficult to detect due to potential time lags of centuries. Thus, there is a distinct risk that Cc may eventually competitively exclude Cf at all landscape scales. As no country in Eurasia obviously wants an invasion of Cc, and as most national conservation laws and international treaties forbid the spread of alien species, we advocate that the precautionary principle be adhered to and an attempt to eradicate Cc from Eurasia be seriously considered. Successful eradication is still possible if the will to do so exists. Here, we outline an eradication strategy.

Key words: alien species, Castor canadensis, Castor fiber, competition, competitive exclusion, eradication, invasion

Howard Parker & Frank Rosell, Faculty of Arts and Sciences, Department of Environmental and Health Studies, Telemark University College, NO-3800 Bø i Telemark, Norway - e-mail addresses: howard.parker@hit.no (Howard Parker); frank.rosell@hit.no (Frank Rosell)
Petri Nummi, Department of Forest Sciences, P.O. Box 27, FIN-00014 University of Helsinki, Finland - e-mail: petri.nummi@helsinki.fi
Göran Hartman, Department of Ecology, Swedish University of Agricultural Sciences, P.O. Box 7002, SE-750 07 Uppsala, Sweden - e-mail: goran.hartman@nvb.slu.se

Corresponding author: Howard Parker

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Motives for the purposeful introduction of alien mammalian species to new environments are many including e.g. new game to hunt or trap, control of overabundant pests, new sources of wild or domestic food or simply the addition of familiar fauna to a new homeland (Wittenberg & Cock 2001). However, the introduction of a look-a-like alien to help reestablish a nearly extirpated native species has rarely been one of them. The North American beaver *Castor canadensis* (Cc) was introduced to Eurasia in 1937 to supplement an ongoing reintroduction of beaver to Finland instigated in 1935, initially with Eurasian beaver *C. fiber* (Cf) from neighbouring Norway (Lahti & Helminen 1974). At the time, the taxonomical status of beaver from both continents was still in question. For the past two centuries, many leading zoologists had considered all beavers to belong either to one species or two subspecies (Morgan 1868). It is therefore understandable if those who conducted the reintroduction were oblivious to the possibility that a new and

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potentially damaging species was perhaps being introduced. At the time, few laymen would have suspected that animals with seemingly indistinguishable exteriors, despite being from different continents, could belong to two different species. It was not until 36 years later that Lavrov & Orlov (1973) determined that the genus *Castor*, in fact, consisted of two species based on different chromosome number (Cf = 48, Cc = 40).

Population development of Cf and Cc in Eurasia

The original range of Cf extended throughout most of Eurasia from the Arctic to the Mediterranean, Atlantic to Pacific, and from coastal waterways to the tree line (Nolet & Rosell 1998). The original range of Cc in North America was equally extensive (Novak 1987). Due primarily to overexploitation between the 16th and 19th centuries, both species were nearly driven to extinction. By the late 19th century, only eight remnant populations of Cf still existed in Eurasia (Halley & Rosell 2002). In Fennoscandia (Norway, Sweden and Finland), the last individual disappeared from Finland in 1868 (Lahti & Helminen 1974) and from Sweden in the early 1870s (Hartman 2011). Norway, however, managed to save a relict population of about 100 individuals (Rosell & Parker 2011). In 1935, 17 Norwegian Cf were released in Finland at five locations; four in the southwest and one in the north (Lahti & Helminen 1974). To continue the reintroduction, more Norwegian beavers were requested but could not be provided. As a substitute, in 1937, Finland obtained seven Cc from the state of New York, USA, including four females. Two pairs were released in southeastern Finland near Sääminki and the remaining three at two adjacent sites in southwestern Finland, in the same area where individuals of Cf had been released only two years previously (Lahti & Helminen 1974). At this time, it was still uncertain how many species of *Castor* actually existed.

Under protection from harvest and in an environment void of beaver for centuries, the two pairs of Cc at Sääminki multiplied rapidly, unhindered by significant predation (Management Plan for the Wolf Population in Finland 2005) or competition from Cf. Starting in 1945, live-trapped individuals from this population were released at new sites in northern Finland and to the east near the Russian border (Lahti & Helminen 1974). From this eastern release, the population spread to the neighbouring Russian state of Karelia (hereafter Karelia) in the early 1950s (Danilov & Kan'shiev 1983). In the following years, many similar releases of Cc into new areas of Finland and Karelia were conducted to stimulate population growth. By 2003, the population in Karelia had grown to an estimated 8,000 (Danilov et al. 2011c). In contrast, releases of Cf in Finland, for reasons unknown, have fared less well (Lahti 1997). Only one small, slowly growing population has developed in southwestern Finland since the first releases in 1935. Just recently, this population has converged with the more rapidly expanding population of Cc



Figure 1. Distribution of the Eurasian (light grey) and North American (dark grey) beavers in western Eurasia. The hatched area indicates the approximate region of population overlap near the Finnish-Russian border.

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from eastern Finland (Lahti 1997; Fig. 1). In 2001, an estimated 1,500 Cf and 12,000 Cc were found in Finland (Nummi 2001a).

In neighbouring Sweden, about 80 Cf obtained from Norway were released at numerous sites between 1922 and 1939. In 1999, the Swedish population was estimated to be about 100,000, extending somewhat discontinuously north to the Finnish border (Hartman 1999; see Fig. 1). In Norway, the small remnant population of Cf increased to the present population of about 70,000 (Rosell & Parker 2011), concentrated to the east and southeast (Halley & Rosell 2002; see Fig. 1), with no individuals known to exist in the north near the Finnish border (Parker 2005, Rosell & Parker 2011). Despite numerous introductions of Cc to northern Finland during the last decades (Danilov et al. 2011c), only a small population of < 50 individuals is believed to presently exist there (A. Ermala, pers. comm.; see Fig. 1). Likewise, numerous introductions of Cf to northern Norway have not been successful (Parker 2005). Thus, northern Fennoscandia is presently open for unhindered colonisation of dispersing Cc from further south, a situation Swedish and Norwegian conservation authorities have observed with concern (Rosell & Parker 2011). In contrast, the vast region south and east of Karelia is presently occupied only by Cf (see Fig. 1), with the exception of three small populations of Cc introduced near the Pacific coast (Nolet & Rosell 1998). Outside of Fennoscandia, numerous cases of the intentional release or unwanted escape of captive Cc have occurred since 1926 (Table 1). With the exception of introductions in Russia, none so far have resulted in lasting populations. However, small numbers of Cc still exist at various locations and their removal is an ongoing process (Dewas et al. 2012).

Since its introduction in 1937, the Fennoscandian population of Cc has, with few exceptions, been able to develop unhindered by competition from Cf and is now centred in south-central Finland and Karelia (see Fig. 1). Within the past decade, however, populations of the two species have converged at two fronts, one in southwestern Finland and the other one in Karelia (see Fig. 1). According to Gause's competitive exclusion principle (Gause 1934), two species with identical niches cannot coexist indefinitely. Now, for the first time since the introduction of Cc to Finland in 1937, the outcome of competition between the two species can be observed and studied along the two population fronts. The imminent question is whether coexistence or competitive exclusion will ultimately result, with the possible extirpation of Cf on a regional or even continental scale.

In this article, we review 1) the behavioural, ecological and life history characteristics of potential competitive importance for both species, 2) the published accounts of contact between the two species for signs of competitive advantage, 3) the role of competition as a cause of native mammal extinction, and 4) the international legal aspects of this conflict. We then outline a strategy for the possible containment and eventual eradication of Cc from Eurasia.

Methods

Both higher fecundity through more rapid population growth (Hastings 1996, Williamson & Fitter 1996, Sakai et al. 2001) and larger body size during aggressive encounters (Parker 1974, Smith & Parker 1976) are likely to incur competitive advantage. As the original extensive latitudinal distributions of both species would imply considerable variation in body size throughout their respective ranges (McNab 1971), and because reproduction in Cc is known to vary considerably with habitat quality (Novak 1987), we chose to compare data on the life history traits of populations only from Fennoscandia and the bordering Karelia-Leningrad region.

We compared the adult body size (i.e. body length excluding the tail and body mass including the tail) and fecundity (foetus number) of both species from studies of wild populations. Adults are animals ≥ 2 years of age unless otherwise stated. We included both sexes in the adult mass calculation for both species, as body size does not vary significantly between the sexes (Novak 1987, Danilov et al. 2011b). In addition, both sexes participate in territorial defence (Campbell et al. 2005), an important aspect of species competition. All our data are from animals trapped or shot during the fall-to-spring harvest season. Means are shown with $\pm$ 1 standard deviation (SD).

Comparative ecology and life history

Ecology

Both species originally occupied a wide range of habitats (Novak 1987, Rosell et al. 2005) and are very similar in morphology, behaviour and ecology (Djoshkin & Safonov 1972, Danilov & Kan'shiev 1983, Novak 1987, Nolet & Rosell 1998, Rosell et al. 2005, Danilov et al. 2011a,b). Of particular interest

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Table 1. History and present status of the North American beaver either purposely released or known to have escaped from captivity in Europe and Asia.

Country	Origin (number involved)	Year	Present population	Reference
Austria				
East of Vienna	Nursery of Brain Anatomy Institute in Bern (12-15)	1978-1979	Probably extinct	Sieber & Bauer 2001
Styria	Animal and Nature Park, Herberstein	1986?	Probably extinct	Sieber & Bauer 2001
Belgium	Probably Eifel-Zoo in Prüm (Germany) or illegal release	1998-2000	Still present?	Michaux et al. 2011, Dewas et al. 2012, Benoît Manet, pers. comm.
France	Private park near Paris (3)	1975	Extinct	Dewas et al. 2012
Germany[1]				
North Rhine-Westphalia	Breeding farm at Popielno, Poland (6)	1981 and 1989	Still present?	Dewas et al. 2012
Rheinland-Palatinate	Probably Eifel-Zoo in Prüm (Germany) or illegal release	1994 (in Trier)	Both reproductive and sterilised individuals present	Dewas et al. 2012
Bavaria	Breeding farm at Popielno, Poland[2]	1966	No established sites ever verified[3]	G. Schwab & S. Venske, pers. comm.
Hungary	Bad Kissingen Wildpark, Bavaria (7) Animal and Nature Park, Herberstein	1991-1993, 1990s	Probably extinct? Still present?	Bozsér 2001, Schwab & Lutschinger 2001, Bajomi 2011
Luxembourg	Probably Eifel-Zoo in Prüm (Germany) or illegal release	Before 2006	All established sites eradicated (spring 2012), recolonisation by new immigrants is suspected	Michaux et al. 2011, J. Herr & L. Schley, pers. comm., Dewas et al. 2012
Poland	From USA to Masuria (a few)	1926	Extinct (1979)	Zurowski 1962, 1965, 1980, Djoshkin & Safonov 1972
Russia				
Unknown locality	Unknown origin (10)	1927-1933	Unsuccessful	Safonov 1975
North-West Federal District	Many immigrants from Finland	1950s	> 8000	Ivanov 1975, Saveljev 1989
(Leningrad Oblast' and Karelia Republic)	Introductions from Karelian Isthmus to Karelia (115) and Leningrad Oblast' (151)	1964-1984	Successful	Danilov 2009, Danilov et al. 2011c
Far Eastern Federal District	North-West Federal District (506)	1969-1987	600	Saveljev & Safonov 1999
Khabarovsk Territory	Translocated from Karelian Isthmus (99)	1969, 1971, 1975	100	Safonov et al. 1983, Pavlov & Saveljev 1984, Saveljev 1989, Oleynikov & Saveljev 2009
Amurskaya Oblast'	Translocated from Karelian Isthmus (50)	1976	Apparently extinct the following winter	Pavlov & Saveljev 1984
Sakhalinskaya Oblast'	Translocated from Karelian Isthmus (66)	1980	Extinct	Saveljev 1982, 1989
Kamchatka Territory	Translocated from Karelian Isthmus (256)	1977-1984	200?	Safonov 1977, Lomanova et al. 2009

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Table 1. Continued.

Country	Origin (number involved)	Year	Present population	Reference
Primorski Territory	Translocated from Karelian Isthmus (20) and Karelia (15)	1986-1987	< 50?	Saveljev 1989, A. Saveljev, pers. comm.
Ukraine	From USA, released in Rovno district, Goryn' river basin (former Poland) (7)	1933-1934	Extinct (1957)	Dyozhkin 1960, Safonov 1977, Lever 1985

[1] North American beavers were trapped, sterilised and released.
[2] In theory, there might have been some North American beaver among those obtained from Popielno but none of the 1,500 beavers later trapped in this region were apparently North American (G. Schwab, pers. comm.).
[3] One North American beaver was found dead (road-killed) next to an enclosure missing a North American beaver.

are the results from studies of adjacent populations in northwestern Russia. Initially, Danilov & Kan'shiev (1983) reported that for populations of both species living in the area, Cc tended to build more dams and stick-type lodges, better utilise less-preferred grey alder *Alnus incana* and tolerate more marginal habitats than Cf. Results from Finland also suggested that Cc tended to build more dams and stick-type lodges (Ruusila 1997). However, in a later study, Danilov et al. (2011c) repudiated these previously claimed differences, stating that no noteworthy differences in construction activity, landscape use or diet appeared to exist when both species occupied similar habitat. Thus, based on the limited published information presently available from sympatric populations of both species, and in the absence of analyses of niche overlap, we conditionally conclude that niche overlap is virtually complete.

Life history

Larger body size may be an advantage when aggressive encounters occur between competing alien and native mammals (Okubo et al. 1989, Sidorovich & MacDonald 2001). Danilov et al. (2011b) found mean body length to be only slightly (though significantly) shorter for Cc, while mean adult body mass was similar. Other data on the mean body mass of adult Cf confirm this body mass similarity (Table 2). Consequently, Cc appears not to have a size advantage over Cf. However, since competitors of similar size are predicted to engage in aggressive encounters more often (Parker 1974, Smith & Parker 1976), we suspect a high degree of aggression during territorial encounters.

The mean foetus number was less for Cf ($\approx$ 2.5) than for Cc ($\approx$ 4.0; see Table 2), and is mirrored in the differences in mean litter size (young born) for Cf and Cc of 1.9 and 3.2 reported by Danilov (1995), and 2.2 and 4.0 by Danilov et al. (2011a), respectively. Likewise, Rosell & Parker (1995) reviewed the published data for both species on both continents and arrived at a mean colony size of 3.8 $\pm$ 1.0 (N = 13 studies; range: 2.4-5.5) for Cf and 5.2 $\pm$ 1.4 (N = 51 studies; range: 2.7-9.2) for Cc. Thus, the only well-documented life history difference between the two species of potential competitive advantage appears to be higher fecundity for Cc. This may, in part, explain why the population of Cc has grown more rapidly than Cf in Finland (Nummi 2001b).

How invasive is the invader?

Invasion by non-indigenous species is recognised as second only to loss of habitat and landscape fragmentation as a threat to global biodiversity (Allendorf & Lundquist 2003). Biotic invaders are usually defined as species that not only establish a new range in which they proliferate and spread, but also persist to the detriment of the environment (Mack et al. 2000). Cc has proliferated and spread in Eurasia, but has it been detrimental to the environment there? So far, it has caused no known extinctions or transmitted damaging parasites or pathogens (Rosell et al. 2001). Damage to forests and farmland in Eurasia from tree felling and inundation following dam building is caused by both species. Though Cc reportedly builds more dams than Cf (Danilov 1995, Ruusila 1997), Danilov et al. (2011c) detected no such difference. Thus, Cc does not appear to cause appreciably more damage than Cf. Though genetic introgression becomes a problem when alien and native species hybridise successfully (Groning & Hochkirch 2008), no live-born Cc/Cf hybrids are known to have occurred (Lavrov 1996), and attempts to deliberately produce them in captivity have so far failed (Zurowski 1983), despite observed copulations (Lavrov & Orlov 1973). In short, Cc to date has not caused these types of problems.

Outcome of species contact to date

At three localities in Finland to which both species

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Table 2. Comparative life history characteristics of adult North American and Eurasian beavers collected in Fennoscandia and the adjacent Russian Karelia-Leningrad region during winter and spring. Mean adult body length (excluding the tail) and mass (including the tail) are pooled for both sexes.

Species	Reference	Adult body		Foetus number	Notes
		Length (cm)	Mass (kg)		
C. canadensis	Lahti & Helminen (1974)			Mean = 4.7 Range: 1-8 N = 9	Growing population, for animals ≥ 2 years old.
	Ruusila et al. (2000)			Mean = 3.7 N = 24	Same population as Lahti & Helminen (1974), but now reportedly at carrying capacity; for animals ≥ 2 years old.
	Danilov et al. (2011b)	Mean = 76.8 Range: 69.0-85.0 N = 34	Mean = 17.2 Range: 13.8-23.1 N = 34		For animals classified as adults (no age stipulated) from the Karelia region.
C. fiber	Danilov et al. (2011b)	Mean = 80.5 Range: 76.0-86.0 N = 41	Mean = 17.8 Range: 14.4-24.0 N = 41		For animals classified as adults (no age stipulated) from the Leningrad region.
	Our study		Mean = 17.0 Range: 9.0-25.6 N = 107	Mean = 2.4 Range: 1-5 N = 32	For animals ≥ 2 years old.
	Mörner (1990)			Mean = 2.5 Range: 1-5 N = 43	Includes only individuals ≥ 16 kg, i.e. some lighter, primiparous 2-year olds were likely excluded.
	Our study		Mean = 17.6 Range: 11.0-26.0 N = 149		Data provided by Sten Lavsund for animals ≥ 3 years old

were introduced concurrently, Cf quickly disappeared leading to the preliminary conclusion that Cc might be the better competitor (Lahti 1997, Nummi 2001b). However, three repetitions involving few individuals are insufficient to base a conclusion of competitive exclusion on (Nummi 2001b). In contrast, Danilov (1995) related an incidence where a small population of Cc in Poland disappeared following contact with Cf. However, the best evidence for competitive dominance to date was recently reported by Danilov et al. (2011a). Along a broad front in Karelia where populations of the two species have recently converged, sites where Cc were earlier released and became established are now occupied exclusively by Cf that recently arrived, suggesting that Cf may be the better competitor. The mechanisms behind this apparent displacement process are presently unknown (Danilov et al. 2011a). Therefore, the question of which species might have the competitive upper hand is still open, though this new information gives ground for optimism.

Is competition from invasive congeners a common cause of native extinction?

Whereas introductions of predators and pathogens have caused numerous and well-documented extinctions of native species, particularly in spatially restricted environments like islands and lakes, few instances of extinctions of natives can be attributed to competition from invading species (Ebenhard 1988, Davis 2003). It is possible, however, that competition-driven extinctions involve considerable time lags (Crooks 2005) and require more time than the predation-driven extinctions, or that biological invasions are more likely to threaten species through intertrophic than intratrophic interactions. A unification of biodiversity theory and extinction data sets suggests that, compared to intertrophic interactions and habitat loss, competition from introduced species is not likely to cause the extinction of natives at either the global, metacommunity or most community levels (Davis 2003).

In the light of this, it seems unlikely that compe-

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tition from Cc will eventually lead to the extinction of Cf throughout Eurasia. However, invasion histories tend to be unique (Richardson et al. 2000) and time lags may play an important role in the extinction process (Crooks 2005). E.g. the invasive North American grey squirrel *Sciurus carolinensis* and North American mink *Neovison vison* (until recently *Mustela vison*) have gradually been replacing populations of native red squirrel *S. vulgaris* in Great Britain and Italy (Wauters et al. 2002, Martinoli et al. 2010) and European mink *M. lutreola* throughout Europe for the past century (Maran & Henttonen 1995, Maran et al. 1998). In Finland and Karelia, the initial time from the introduction of Cc to the convergence of the two species encompassed approximately 60 years during which time Cc expanded rapidly, unhindered by competition from Cf. As the large scale extirpation of native mammal populations by an alien often involves centuries (Lawton & Godfray 1990, Kamler & Ballard 2002, Reid 2011), a competitive exclusion of Cf by Cc could take time. As aptly stated by Crooks (2005) "Recognition of the phenomenon of long lags before sudden changes in invader dynamics also suggests that we adopt a strict precautionary principle: we should assume that any invader has the potential for undesirable effects and that long periods of seemingly consistent behavior can be poor predictors of what invaders will do in the future".

Both theoretical and experimental studies of interspecific competition conclude that niche differentiation or different activity patterns, foraging behaviour or habitat use among competing species are necessary for competitive coexistence in communities influenced by density-dependant processes (Macarthur & Levins 1964, Schoener 1974, Wauters et al. 2002). As Cc and Cf apparently show few differences in these characters, competitive coexistence seems unlikely. However, without sufficient field data on their comparative ecologies during sympatry, the long-term outcome of competition between these two species is impossible to predict.

Legal aspects

We assume that no other Eurasian country wishes an invasion of Cc, and that most have national environmental laws to help hinder alien species invasions. Additionally, several international conventions, which most European states have signed, aim to regulate the hindrance, spread and control of alien species invasions both within and between member states (Genovesi 2001). Consequently, hindering the spread of Cc between countries has a strong ethical and legal foundation.

Is the local extirpation or total eradication of Cc in Eurasia desirable, or even possible?

Due to apparently near total niche overlap, the chance that major niche partitioning and competitive coexistence will result seems unlikely (Macarthur & Levins 1964, Schoener 1974), even in the highly heterogeneous collection of riparian habitats which both species are known to occupy. Though the extinction of Cf appears unlikely, extirpation of local populations may occur if indeed Cf proves to be the weaker competitor, while Cc may colonise vacant habitats faster due to its greater fecundity. Accordingly, the precautionary principle dictates that the local control of Cc, or an attempt at total eradication, should be considered.

We know that the large scale extirpation of Cc is technically possible, at least when commercially motivated, as it was accomplished throughout most of the species' range during nearly 400 years of the North American fur trade (Novak 1987). More recently, both regulated trapping (Jonker et al. 2006) and hunting with firearms (Parker et al. 2002, Parker et al. 2007) have proven effective in reducing beaver density. Likewise, hunting and trapping appear to have led to slower than expected population growth of both Cc and Cf in Finland during recent decades (Ermala 1997, Lahti 1997). Spring hunting, which is the main harvest form for beaver in Fennoscandia, selects for adults, particularly pregnant females (Parker et al. 2002). Therefore, spring hunting should prove particularly effective in reducing or aiding in eradicating populations of Cc in Finland. Occupied lodges are highly visible from the air or ground in autumn after food caches have been collected (Novak 1987), allowing trappers and hunters to effectively locate and remove animals. Finnish hunters are well organised and accustomed to assisting with wildlife research and conservation (Lindén et al. 1996). In Russia, trapping and hunting of furbearers is still a common and accepted harvest form (Safonov & Saveliev 2001). Thus, both Finland and Russia seem well-suited culturally, socially and technologically to carry out a successful eradication of Cc. The ongoing plan for the eradication of Cc from the Fuegian Archipelago of South America could be of interest in this respect (Anderson et al. 2012).

The eradication of mammals has proven most successful when conducted on islands (Courchamp et al. 2003), as exemplified by the eradication of

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muskrats *Ondatra zibethicus* and coypu *Myocastor coypus* from Great Britain (Gosling & Baker 1989). Though the eradication of Cc would occur in a mainland environment, the main population is limited to an isolated area of the continent bounded in part by sea, or by land presently unoccupied by beaver, as in northern Finland and northwestern Russia (see Fig. 1). This should facilitate the eradication process. The location and removal of the small groups of Cc presently found at several sites in Eurasia, e.g. in Luxembourg and Belgium (Dewas et al. 2012), should present no major problem. Unfortunately, in areas where the two species presently overlap, eradication will likely involve the removal of some individuals of Cf as well. If, however, Cf excludes Cc where populations converge, as suggested by Danilov (2011a), active eradication may only be necessary to prevent the future spread of Cc to the northern regions of Finland, Sweden, Norway and Karelia. In summary, Cc can be eradicated from Eurasia if the will to do so exists, particularly if Cf proves to be the dominant competitor. It is vital that the question of competitor dominance be investigated.

An eradication strategy

Here, we have chronologically outlined a strategy for the eradication of Cc from Eurasia, which is in accordance with the IUCN Invasive Species Specialist Group's recommendations for eradications (Veitch et al. 2011). Methods other than hunting, dead-trapping, reintroduction and population monitoring are likely to be unnecessary.

Removal of small populations

Small, isolated populations or groups of Cc throughout the continent must be located and removed immediately before they spread. Individuals suspected to be Cc can be live-captured and the species determined based on the sex and colour of the anal gland secretion of the individuals (Rosell & Sun 1999) or tested genetically (Kuehn et al. 2000, Dewas et al. 2012). Those positively identified as Cc could be either sterilised (Dewas et al. 2012) or euthanised. This is particularly important in northern Finland where the spread of Cc to neighbouring Sweden and Norway is imminent. It is important that Great Britain remains free of Cc.

Conduct crucial research

Research designed to answer the following core questions important for the eradication process must be implemented without hesitation in Karelia and southwestern Finland where the two species have converged: 1) Is competitive exclusion occurring, and if so, which species of the two is being excluded?, 2) Do dispersing individuals of Cc manage to successfully infiltrate areas occupied by Cf, find mates, breed successfully and establish viable populations?, 3) Is interspecies mate-bonding or even successful hybridisation occurring?, and 4) What effort is needed to remove the subpopulations in question? Considerable opportunities exist here to explore some of the basic processes involved in coexistence ecology and population extermination.

Establish an eradication strategy

If dispersing Cc filter through the broad region to the south and east of Karelia occupied by Cf and reproduce successfully then the effective eradication of Cc from this region may be impossible, as selectively removing them from a mixed population would be difficult at best. Alternatively, if dispersing individuals of Cc are effectively stopped by this 'wall' of Cf, as suggested by Danilov et al. (2011a), the eradication process should prove far simpler. If Cf effectively excludes Cc in some manner through competition, then it should be possible to 'behaviourally contain' the entire population of Cc to northwestern Europe by gradually surrounding it with a seemingly impenetrable wall of Cf. Conceivably, this surrounding population might then gradually advance inward, excluding and eventually extirpating all Cc from the region. Alternatively, all individuals of both species could be rapidly removed from the region of overlap.

The eradication process could be accelerated by 1) overharvesting Cc by e.g. eliminating quotas, allowing year-round harvest or even allowing night-hunting with lights, and 2) enhancing the population growth of Cf at specific locations by protecting all but nuisance animals until population goals have been achieved. The overharvest of Cc should occur throughout its range simultaneously, but special effort must be directed from population borders towards population centres, thereby gradually reducing the area occupied by Cc. To ensure that pockets of Cc do not survive along population borders, systematic population monitoring will be necessary. Once all remnant individuals of Cc have been removed from northern Finland, extensive reintroductions of Cf to the unoccupied regions here and in Karelia, Sweden and Norway should be considered.

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Throughout the eradication process, it will be necessary to maintain an unoccupied region between populations of the two species, since once they mix, selective removal becomes difficult. Instead of lethally removing all nuisance Cf, many could be live-trapped and released to the north, employing well-established capture methods (Novak 1987, Rosell & Kvinlaug 1998, Rosell & Hovde 2001). Thus, through a combination of selective harvesting of Cc and extensive live-capture and translocation of Cf, it should be possible to gradually extirpate Cc from northwestern Europe.

Plan execution

Good planning and management including e.g. risk analysis, clear lines of responsibility and authority and institutional and public support greatly improve the chances of eradication success (Gosling & Baker 1987, 1989, Courchamp et al. 2003). The eradication of a charismatic species like the beaver can be particularly difficult for the public to accept, though we expect little public opposition in Finland and Russia where beaver hunting and trapping are accepted. Finding competent and dedicated hunters and trappers to perform the eradication and monitoring should prove no obstacle, particularly if incentive bonuses are employed (Gosling & Baker 1989).

Conclusion

Because of their extreme biological and ecological similarities, the competitive exclusion of one species by the other may possibly occur in the future. Presently, we lack sufficient ecological knowledge to predict which. Though the complete extinction of Cf throughout Eurasia seems unlikely and could take centuries, local extirpations could occur. As no country in Eurasia obviously wants an invasion of Cc, and since most national conservation laws and international treaties forbid the spread of aliens, we advocate that the precautionary principle be adhered to in this instance and an attempt to eradicate Cc from Eurasia be seriously considered. Successful eradication is possible, if the will to do so exists.

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