

## **Paper IV**

1 *Strength of asymmetric competition between predators in food webs ruled by*  
2 *fluctuating prey: The case of foxes in tundra*

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25 **Abstract**

26 In food webs heavily influenced by multi-annual population fluctuations of key herbivores,  
27 predator species may differ in their functional and numerical responses as well as their  
28 competitive ability. Focusing on red and arctic fox in tundra with cyclic populations of  
29 rodents as key prey, we develop a model to predict how population dynamics of a dominant  
30 and versatile predator (red fox) impacted long-term growth rate of a subdominant and less  
31 versatile predator (arctic fox). We compare three realistic scenarios of red fox performance:  
32 (1) *A numerical response scenario* where red fox acted as a resident rodent specialist  
33 exhibiting population cycles lagging one year after the rodent cycle, (2) *a functional response*  
34 *scenario* where red fox shifted between tundra and a nearby ecosystem (i.e. boreal forest) so  
35 as to track rodent peaks in tundra without delay, and (3) *a constant subsidy scenario* in which  
36 the red fox population was stabilized at the same mean density as in the other two scenarios.  
37 For all three scenarios it is assumed that the arctic fox responded numerically as a rodent  
38 specialist and that the mechanisms of competition is of a interference type, in which the arctic  
39 fox is excluded from the most resource rich patches in tundra. Arctic fox is impacted most by  
40 the constant subsidy scenario and least by the numerical response scenario. The differential  
41 effects of the scenarios stemmed from cyclic phase-dependent sensitivity to competition  
42 mediated by changes in temporal mean and variance of available prey to the subdominant  
43 predator. A general implication from our result is that external resource subsidies (prey or  
44 habitats), monopolized by the dominant competitor, can significantly reduce the likelihood  
45 for co-existence within the predator guild. In terms of conservation of vulnerable arctic fox  
46 populations this means that the likelihood of extinction increases with increasing amount of  
47 ungulate carcass in tundra and nearby forest areas, since it will act to both increase and  
48 stabilize populations of red fox.

49

## 50 **Introduction**

51 While much emphasis in ecology has classically been placed on the effects of predators on  
52 prey populations, far less attention has been paid to the effect that predators have on each  
53 other. However, recently interactions between predators have gained increasing attention in  
54 theoretical and empirical studies as potentially important structuring agents of both  
55 communities and food webs (Gurevitch et al. 2000, Polis and Holt 1992, Polis et al. 2004). A  
56 central task in these studies is to identify mechanisms that promote co-existence or  
57 competitive exclusion of species in predator assemblages (guilds) with overlapping prey. For  
58 instance, the mode of interaction may matter; i.e. whether competition is mainly exploitative  
59 (indirect) or involves some degree of direct interference ranging from avoidance behaviours  
60 to intraguild predation (Amarasekare 2002, Palomares and Caro 1999, Polis et al. 1989). In  
61 guilds of carnivorous vertebrates fierce interference interactions are often highly asymmetric  
62 with large-sized species being dominant in contests, and thereby limiting population growth  
63 of small-sized species (Clark et al. 2005, Fedriani et al. 2000, Lindström et al. 1995,  
64 Macdonald and Sillero-Zubiri 2004, Nelson et al. 2007, Switalski 2003, Tannerfeldt et al.  
65 2002). Still, the ultimate outcome of such asymmetric inter-specific contest is likely to be  
66 heavily influenced by the spatio-temporal distribution of the contested resource. Yet,  
67 intraguild competitive interactions remain largely unexplored in situations where the  
68 temporal dynamics of food resources is pronounced.

69         The temporal dynamics of northern terrestrial food webs is often ruled by  
70 pronounced multi-annual population cycles of key herbivores like snow shoe hares or small  
71 rodents (voles and lemming) (Elton 1942). These herbivores represent key prey for guilds of  
72 vertebrate predators (Ims and Fuglei 2005, Korpimäki and Krebs 1996). The various predator  
73 species within these guilds may, however, differ somewhat in terms of the degree of  
74 specialization on habitat and prey, which in turn affects their numerical and functional

75 responses (Andersson and Erlinge 1977, Gilg et al. 2003, Krebs et al. 2001, Wiklund et al.  
76 1999). Consequently, an evaluation of the outcome of asymmetric competition in such a  
77 system must consider the underlying prey dynamics as well as the competing predators'  
78 numerical and functional responses to the prey cycle. For instance, if the dominant predator  
79 species operates as a typical resident specialist (cf. Andersson and Erlinge 1977), and  
80 responds numerically to the prey cycle (i.e. with a time-delay), the largest effect on  
81 subdominant competitors could be expected in the crash phase of the prey cycle. On the other  
82 hand, if the dominant species responds like a generalist that functionally shifts habitat and/or  
83 diet to track peak prey density populations, the greatest effect on the subdominant species  
84 could be expected in the increase and peak phases of the cycle. However, while the phases of  
85 the prey cycle with the most intense competition for different numerical and functional  
86 responses of the dominant predator may be rather straightforward to deduce, the outcome in  
87 terms of long-term viability of the subdominant species, and thus the likelihood for species  
88 co-existence within guilds, is in need of more elaborate analysis. In this study we provide  
89 such an analysis by means of modelling. We use a pair of interacting fox species in tundra  
90 ecosystems as a specific case. The analytical framework may, however, apply more broadly  
91 to competitive interactions between predators depending on strongly fluctuating prey  
92 populations.

93         As with other closely related canids (Clark et al. 2005, Fedriani et al. 2000, Nelson et  
94 al. 2007, Switalski 2003), competition between arctic fox (*Vulpes lagopus*) and red fox  
95 (*Vulpes vulpes*) can be expected to be fierce. Indeed, many studies have indicated that the  
96 larger sized red fox can expel the arctic fox in cases where their distribution range comes to  
97 overlap (Chirkova 1968, Killengreen et al. 2007, Linnell et al. 1999, Tannerfeldt et al. 2002).  
98 The importance of competition between the two fox species has been particularly emphasized  
99 in Fennoscandia where the decline of the arctic fox to near extinction, at least partly, have

100 been attributed to the expansion of the red fox into the mountain tundra (Kaikusalo and  
101 Angerbjörn 1995, Killengreen et al. 2007, Tannerfeldt et al. 2002). However, similar  
102 replacement of the arctic fox, by the red fox, appears to take place in many other places in the  
103 circumpolar tundra (Chirkova 1968, Hersteinsson and Macdonald 1992, MacPherson 1964,  
104 Marsh 1938).

105 In regions where vole and lemming cycles prevail, both fox species prey to a large  
106 degree on small rodents (Elmhagen et al. 2002). Moreover, both species respond numerically  
107 to rodent dynamics and can themselves exhibit population cycles that mirror the cycle of their  
108 rodent prey (Angerbjörn et al. 1995, Butler 1951, Elton 1942). However, while the arctic fox  
109 appears to be a resident rodent specialist in inland tundra ecosystems (Angerbjörn et al.  
110 1999), the red fox is capable of utilizing a greater span of suitable habitats, for instance, the  
111 boreal forest (Hersteinsson and Macdonald 1992). As a result, the red fox is capable of  
112 displaying a functional response in both habitat and prey when such alternatives are available.

113 In this paper we outline three realistic ecological settings, which yield different  
114 scenarios of numerical and functional responses to cyclically fluctuating prey in the dominant  
115 generalist predator (e.g. red fox). We then use modelling to predict the long-term impact of  
116 asymmetric competition on the subordinate predator (e.g. arctic fox).

117

## 118 **Modelling framework**

119 The general framework of our modelling consists of three interlinked compartments (Fig. 1).  
120 The first model compartment provides realizations of small rodent prey dynamics that  
121 phenomenologically simulate the characteristics (i.e. cycle period and amplitude) of typical  
122 vole and lemming cycles (Stenseth 1999). The two other compartments model the dynamics  
123 of the two fox species (Fig. 1). The arctic fox dynamics is always modelled as a resident

124 specialist with a pronounced numerical response (i.e. population dynamics) that is entirely  
125 driven by the amount of available rodent prey (Angerbjörn et al. 1999). In this case, the arctic  
126 fox population exhibits cycles with a typical one-year time lag relative to the prey cycle. The  
127 red fox dynamics varies, however, among the three ecological scenarios considered. The first  
128 scenario may apply to a setting in which large tracts of tundra is located far from adjacent  
129 ecosystems. In this case the red fox (like the arctic fox) possesses the dynamical attributes of  
130 a resident specialist (Englund 1970). We term this the *numerical response scenario*. In the  
131 second scenario, we assume that the red fox has access to an alternative nearby habitat (e.g.  
132 boreal forest) which is more profitable than tundra in terms of alternative prey resources in  
133 the low phase of the rodent cycle. In the late increase and peak phase of the rodent cycle,  
134 however, the red fox performs functional habitat switching (cf. Mysterud and Ims 1998) in  
135 the sense that it invades the nearby tundra (Elmhagen 2003). In this scenario, which we term  
136 the *functional response scenario*, the red fox has a cyclic abundance dynamics in tundra  
137 similar to the numerical response scenario, but with the exception that the response to rodent  
138 dynamics will be instant (i.e. direct prey tracking; cf. Korpimäki 1994) and not delayed with  
139 a one-year time lag. In the third and final scenario we assume a stable red fox population in  
140 tundra owing to some external food subsidy: i.e. *the constant subsidy scenario*. Likely  
141 candidates for such subsidies are overabundant semi-domestic reindeer populations providing  
142 carcass resources (Ims et al. 2007) or subsidies from marine food webs in coastal tundra  
143 (Roth 2003).

144 For all scenarios we assume that red fox impacts population growth in arctic fox  
145 through interference competition by which the red fox excludes the arctic fox from the most  
146 resource rich sites on the tundra (cf. Bailey 1992, Killengreen et al. 2007, Tannerfeldt et al.  
147 2002). As a consequence the red fox affects the population growth rate of the arctic fox by  
148 reducing the amount of prey available to the arctic fox. This reduction of available prey, and

149 resultant negative impact on arctic fox growth rate, increases proportionally with the  
150 prevailing abundance of red fox.

151         Technically, both the modelling of the rodent dynamics and its link to the numerical  
152 dynamics of foxes as resident specialists follows Henden et al. (2008), which used a two-  
153 compartment version of the model to analyse population viability of arctic fox as a function  
154 of different attributes of small rodent population cycles. In short, small rodent dynamics is  
155 simulated by a stochastic second order autoregressive model, while the resultant arctic fox  
156 dynamics is obtained from a age-structured demographic model in which yearly matrices of  
157 demographic parameters are made dependent on the prevailing rodent density (for more  
158 details see Henden et al. 2008). In the present analysis we chose autoregressive coefficients to  
159 yield small rodent dynamics with a typical 4-year cycle period. This in turn yields a long-  
160 term stochastic growth rate  $\lambda = 1.073$  for the arctic fox (Henden et al. 2008), when no  
161 competition with red fox is included in the model. In case of the numerical response scenario  
162 of the extended three-compartment model, the red fox compartment is structurally equivalent  
163 to that for the arctic fox. However, the parameters of the demographic functions (Table 1)  
164 were adjusted to fit with what is known about red fox demography from the literature. As a  
165 result red fox reproduction and survival is somewhat less sensitive to abundance of rodents  
166 (see Table 1). To verify that the combination of parameter values was reasonable for the red  
167 fox we compared the resultant age structure from the model with empirical data.

168         In the case of the functional response scenario, red fox abundance was simulated by  
169 using the time series generated from the numerical response scenario, but shifted one year as  
170 to obtain the non-delayed response (i.e. direct prey tracking). Thus, the functional and  
171 numerical response scenarios differ only in terms of the timing of the peak of red fox  
172 abundance and impact on arctic fox population growth. Finally, the stable red fox abundance



173 of the constant subsidy scenario was set equal to the mean abundance generated for the two  
174 other dynamic scenarios.

175 We assumed an inverse sigmoid function (see Fig. 2) for linking the prevailing abundance of  
176 red fox to a percentage reduction of small rodent prey available to the arctic fox. Since the  
177 parameters of this function (see Table 1), which determines the severity of the impact of  
178 interference competition on yearly growth rates in the arctic fox, could not be inferred from  
179 empirical data, we assessed the sensitivity of our results to the chosen parameter values. We  
180 did this by using functions with two different shapes (i.e. strength of the relationship), but  
181 with the same area under the function.

182 The results of the modelling will be presented in terms of long-term stochastic growth  
183 rate of the arctic fox obtained by simulating 10000 years in each scenario (Caswell 2001).

184

## 185 **Results**

186 The assumptions and selected parameter values for the arctic fox compartment of the model  
187 are thoroughly explored in Henden et al. (2008). In case of the red fox in the present  
188 simulation we found that the numerical response scenario gave an estimated age-structure for  
189 red fox of approximately 47 % juveniles (individuals < 1 year old) and 53 % adults. This is in  
190 line with that reported by Coman (1988) in a study of red foxes killed in Australia, and a  
191 study of red fox removal in north-eastern Norway where the equivalent figures were 46% and  
192 54 % (Killengreen et al. unpublished). Thus, our model of red fox seems to mimic red fox  
193 demography observed in natural populations.

194 The assumed proportional reduction of small rodent prey available to arctic fox,  
195 owing to interference competition with red fox (Fig. 2, Table 1), gave a substantial decrease  
196 in the long-term population growth rate ( $\lambda$ ) of the arctic fox in all scenarios (i.e. compare the

197 estimated  $\lambda$  for the three red fox scenarios with the estimate without competition in Fig. 3).  
198 However more interestingly, the outcome of the three scenarios differed substantially. The  
199 strongest impact of competition was obtained in the scenario where a stable abundance of red  
200 fox was present in tundra (i.e. the constant subsidy scenario), whereas the weakest impact  
201 was seen when the red fox displayed the numerical response typical of a resident specialist  
202 predator (Fig. 3). The scenario in which the red fox displayed a functional shift in habitat,  
203 according to the prevailing small rodent density in tundra, gave an intermediate impact  
204 compared to the two other scenarios.

205 In general, these results was mostly insensitive to the shape of the functional  
206 relationship linking red fox abundance to reduced availability of prey and consequently the  
207 deteriorated demographic conditions for arctic fox. The only exception was for the constant  
208 subsidy scenario, where the steep relationship (cf. Fig. 2) resulted in a lower long-term  
209 growth rate for the arctic fox than the slow one. Clearly, this difference was brought about by  
210 the mean abundance of red fox intersecting with the curve at a higher reduction in the  
211 steepest version of the function (c.f. Fig. 2).

212

## 213 **Discussion**

214 We have documented that strongly asymmetric interference competition between species  
215 exploiting a cyclically fluctuating resource can yield different likelihoods of long-term  
216 persistence of the subordinate competitor, depending on the ecological context modifying the  
217 population dynamics of the dominant competitor. Although we have used two fox species  
218 belonging to tundra food webs ruled by cyclically fluctuating rodent populations as the case  
219 study for the model analysis, our predictions may apply to other predator guilds in similar  
220 ecological contexts. Below we first discuss the assumptions made regarding the performance

221 of the competing predators and the different ecological settings and scenarios explored. Then,  
222 we turn to the predictions derived from the modelling and their implications.

223

## 224 **Assumptions**

225 Predators typically differ in the degree of specialization on prey, ranging from obligatory  
226 specialists to full generalists (Andersson and Erlinge 1977). In food webs ruled by cyclic  
227 population dynamics of key herbivores, such as small rodents or snow shoe hares, some  
228 predators can act as *facultative specialists* (Roth et al. 2007) or *actual specialists* (Elmhagen  
229 2003). This means that they specialize on the cyclic herbivore in regions where such cycles  
230 prevail, whereas they act as generalists in other regions and ecological settings. Both fox  
231 species considered in this study are facultative specialists. The red fox is an extremely  
232 versatile predator that inhabits a wide range of habitats, ecosystems and biomes, and thereby  
233 preys on whatever available in the various settings (Macdonald 2000). The arctic fox is  
234 restricted to the tundra biome, but can rely on alternative prey items to small rodents (e.g.  
235 marine subsidies) whenever such alternative resource are more available (Macdonald 2000).  
236 However, the most common setting for arctic fox populations, in the vast circumpolar tundra  
237 zone, is the one in which they depend on cyclic rodent populations. In that case, their  
238 population dynamics show the typical signature of a small rodent specialist; i.e. cyclic  
239 fluctuations lagging one year behind their prey (Angerbjörn et al. 1999, Ims and Fuglei  
240 2005). Similar dynamics have been reported for the red fox in northern regions (Butler 1951,  
241 Elton 1942, Henden et al. 2008), thus verifying that both fox species may act as specialist  
242 predators according to our numerical response scenario. Moreover, as entire guilds of  
243 predators have been shown to respond synchronously to both small rodents (Pitelka et al.  
244 1955) and snow shoe hares (Krebs et al. 2001), this scenario may apply to several other  
245 competing predators as well.

246 Owing to its wide habitat spectrum and diverse food web affiliations, we outlined an  
247 alternative functional response scenario for red fox in tundra. In this scenario, which is likely  
248 to apply to contexts where more productive and stable food webs are situated nearby tundra, a  
249 direct tracking of rodent peaks on the tundra is possible for a predator capable of performing  
250 habitat shifts. Although less empirical information is available for such “migration mediated  
251 dynamics” in the red fox, Butler (1951) suggested events of influx of red fox into the arctic  
252 tundra from adjacent boreal forest in Canada. In Fennoscandian mountain tundra, which is  
253 normally imbedded in large tracts of boreal forest, a similar non-delayed response to lemming  
254 peaks in red fox has become evident from efforts made to remove red fox from mountain  
255 tundra in the Swedish-Finnish arctic fox conservation programme (SEFALO 2004,  
256 Angerbjörn and Hellström, unpublished data). More generally, our functional response  
257 scenario applies to the response of nomadic specialist predators (usually very mobile avian  
258 predators) capable of rapid tracking of cyclic peaks of prey in time and space (Ims and Steen  
259 1990).

260 In a final scenario we explored the effect of stabilized dynamics of the dominant  
261 predator (i.e. the red fox) owing to some external resource subsidy (e.g. in terms of terrestrial  
262 carrion or marine resources). Clearly, the subdominant predator (i.e. the arctic fox) is equally  
263 capable of utilizing such subsidies. However, given that the demography of the arctic fox is  
264 not directly influenced by the subsidy in our model, we have implicitly assumed that the  
265 dominant predator (when present) monopolizes the subsidy. Accordingly, studies of  
266 scavenger guilds have shown that contests over carrion can indeed be highly asymmetric  
267 (Selva and Fortuna 2007, Selva et al. 2003, Selva et al. 2005).

268 In lack of detailed information on the dynamics of interference competition in the  
269 different scenarios, we assumed the same phenomenological outcome of asymmetric  
270 competition in all scenarios; namely a proportional reduction of available prey and

271 demographic performance of the arctic fox with increasing red fox abundance. Although  
272 certainly more is to be learned about the mechanisms of competition between the two fox  
273 species from future field studies, we think the assumed impact of competition on the  
274 subdominant predator is essentially realistic if the dominant predator tends to occupy the  
275 most resource rich patches in tundra. Current knowledge about the distribution of red and  
276 arctic foxes, both in low arctic tundra (Killengreen et al. 2007) and mountain tundra (Dalén et  
277 al. 2004, Elmhagen 2003, Frafjord 2003), is in line with the assumption that the red fox  
278 occupies and expels the arctic fox from the most productive parts of the tundra. For instance,  
279 lowland tundra harbours higher rodent densities than high altitude areas, particularly, in peak  
280 years of voles not accompanied by lemmings (Ekerholm et al. 2001).

281

## 282 **Predictions and implications**

283 Our modelling framework yielded the prediction that different temporal dynamics of the  
284 competitively dominant predator (albeit with the same temporal mean abundance) will give  
285 contrasting long-term stochastic growth rate of the subdominant predator. In the two  
286 scenarios with the same cyclic fluctuations of red fox abundance, the arctic fox performed  
287 worse in the functional response than in the numerical response scenario. This means that the  
288 timing of the maximum impact of competition matters. Specifically, maximum impact in the  
289 peak phase of the prey cycle (the functional response scenario) has a larger effect on arctic  
290 fox long-term growth rate than maximum impact in the crash phase (the numerical response  
291 scenario). This kind of phase-dependence has an analogy in the field of life history theory,  
292 where the reproductive value of cohorts has been shown to differ between different cycle  
293 phases in cyclically fluctuating populations (Schaffer and Tamarin 1973, Stearns 1976).

294 By far the largest impact of competition was found in the scenario when the dynamics  
295 of the dominant predator was stabilized owing to an external subsidy. We think that this  
296 effect mainly stems from how the stabilization of red fox abundance affected the mean and  
297 variance of available prey to the arctic fox. Indeed, Henden et al. (2008) found that arctic fox  
298 long-term growth rate was sensitive to the temporal mean and the variance in the prey  
299 dynamics. In particular, the combination of decreased variance and mean abundance of  
300 rodents affects the stochastic growth rate of the arctic fox most negatively. Accordingly, in  
301 the present model the constant subsidy scenario yielded a lower mean (9.8 rodents/ha) and  
302 standard deviation (7.1) of available prey (i.e. when corrected for the reduction imposed by  
303 red fox competition) than the other scenarios. Such an effect is also likely to underlie the  
304 difference between the two dynamic response scenarios, as the numerical response had a  
305 higher mean (11.8) and standard deviation (10.1) than the functional response scenario  
306 (mean=10.9, SD=8.5).

307 The general implication of our work is that interaction strength, in terms of per capita  
308 impact of a dominant competitor on the performance of a subdominant, can be expected to  
309 vary in time and space according to changing ecological contexts. The ecological literature  
310 has many examples, in particular from modelling studies, showing various context-  
311 dependencies in the outcome of interspecific competition (Amarasekare 2002, Amarasekare  
312 2006, Amarasekare 2007, HilleRisLambers and Dieckmann 2003, Nelson et al. 2007). Yet,  
313 we are not aware of previous studies that have examined the context-dependence of  
314 competitive interactions within predator guilds subject to key-stone prey with strong multi-  
315 annual fluctuations (e.g. population cycles).

316 Our study also has some important implications for the specific case of competition  
317 between red and arctic fox, which has attracted a lot of attention from scientists and  
318 managers. The retreat of the arctic fox from the mountain tundra in Fennoscandia

319 (Angerbjörn et al. 1995, Hersteinsson et al. 1989) and southern tundra globally (Hersteinsson  
320 and Macdonald 1992) has been thought to result from increasing abundance of the red fox,  
321 possible owing climatic warming as the main ultimate factor (Fuglei and Ims 2008). Here we  
322 have shown that the (mean) abundance of the red fox is not the only important factor, but also  
323 that the population dynamics matter. Thus a stronger impact of red fox is expected in tundra  
324 with decreasing distance to the boreal forest, not only owing to increased abundance, but also  
325 because of an increased possibility for functional habitat switching in the red fox. However,  
326 the most severe impact of red fox on the arctic fox is to be expected under circumstances  
327 which act to increase the mean and lower the variance in red fox abundance. For instance, the  
328 recent increase in red fox abundance in Fennoscandia appears to result from altered land use  
329 and population control of larger predators (Elmhagen and Rushton 2007) as well as increased  
330 amount of ungulate carrion (Selås and Vik 2007). In particular, we predict that the current  
331 overabundance of semi-domestic reindeer in northern Fennoscandia (Ims et al. 2007), that is  
332 likely to both increase and stabilize red fox populations in tundra, is a key issue that need to  
333 be considered when attempting to conserve the arctic fox.

334

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474 Figure and Table text.

475

476 Fig. 1. Schematic representation of the modelling procedure. A) Rodent population dynamics underlying the  
477 interaction between arctic and red fox. B) Resulting population dynamics (abundance) of red fox, mediated  
478 through the numerical and functional response scenario (1. and 2, respectively). The horizontal line denotes the  
479 constant subsidy scenario (3.). The prevailing abundance of red fox affects arctic fox by reducing (% reduction)  
480 the density of the underlying small rodent dynamics. C) Fluctuations in growth rate of arctic fox from the  
481 reduced demographic conditions (i.e. lower rodent density) given by interference competition with red fox.

482

483 Fig. 2. Functional relationships giving the negative impact of red fox abundance on general demographic  
484 conditions for arctic fox (i.e. reduced rodent density). The percentage reduction derived from a given abundance  
485 of red fox is used to adjust the density of small rodent available for arctic fox. Solid curve depict a steep  
486 relationship, especially at intermediate to high red fox abundance, and stippled curve depict a slightly slower  
487 relationship. Stars denote the percent reduction given by the constant subsidy scenario (i.e. mean red fox  
488 abundance = 75.6 individuals) for the two functional forms, respectively. Note that both functions have  
489 approximately the same area under the curve (see Table 1 for shape parameters).

490

491 Fig. 3. Stochastic growth rates of arctic fox under three different response scenarios of red fox to small rodent  
492 density fluctuations. For each scenario growth rates for two different slopes (circle = steep, triangle = slow) of  
493 the impact of red fox (see Fig. 2) are given. The red horizontal line denotes the growth rate of arctic fox without  
494 interference competition with red fox, whereas the grey stippled line denotes zero growth (i.e.  $\lambda = 1$ ).

495

496 Table 1. Upper part of the table show parameters used in the generation of the logistic functional relationships<sup>1</sup>  
497 relating fox vital rates to small rodent dynamics. Lower part of table show shape parameters used in the  
498 generation of the inverse logistic functional relationship<sup>2</sup> (Fig. 2) linking red fox abundance to the percentage  
499 reduction in small rodent density available for arctic fox.

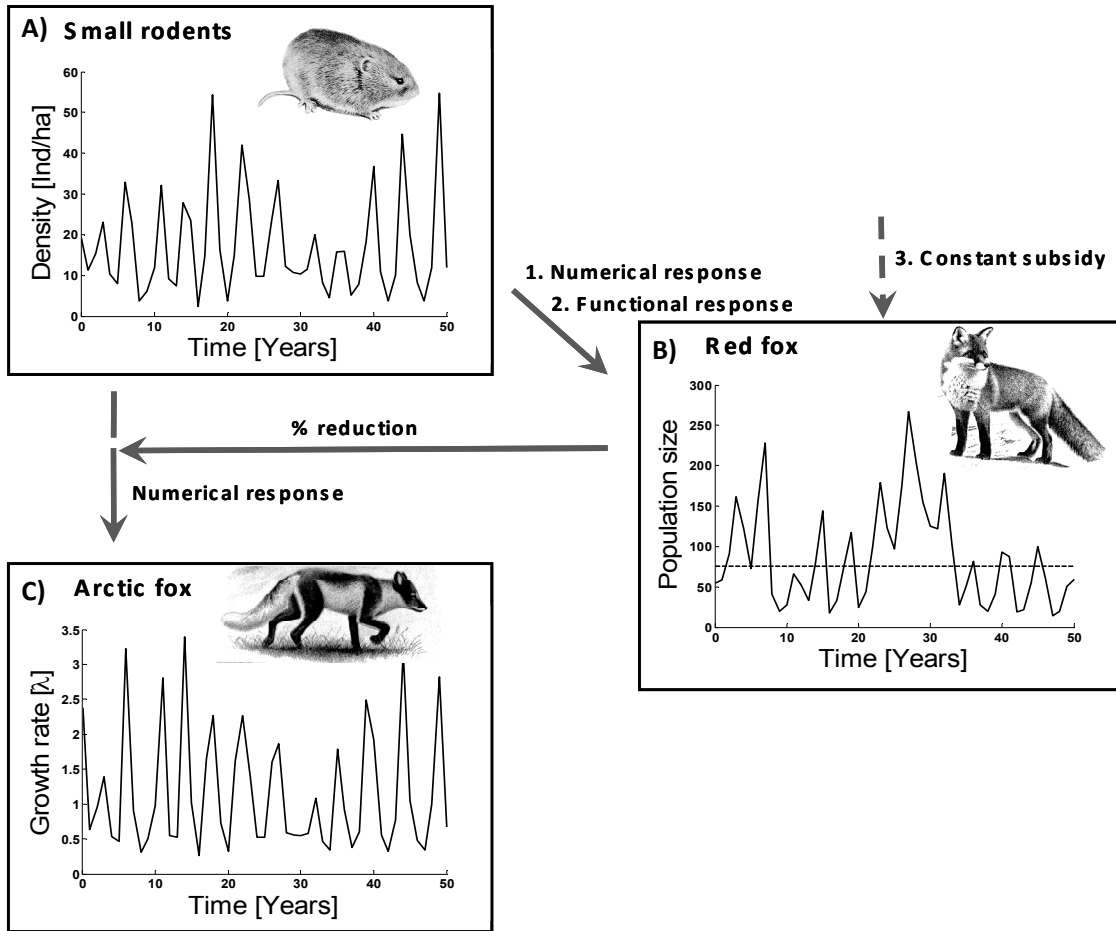
500 Fig. 1.

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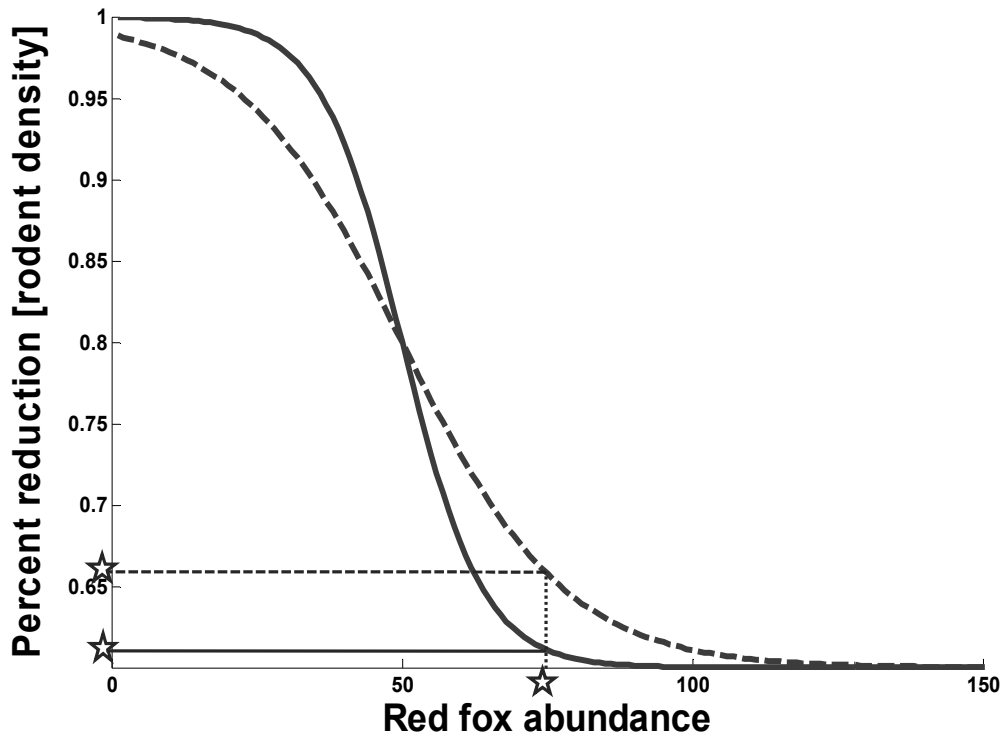
513 Fig. 2.

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528 Fig. 3.

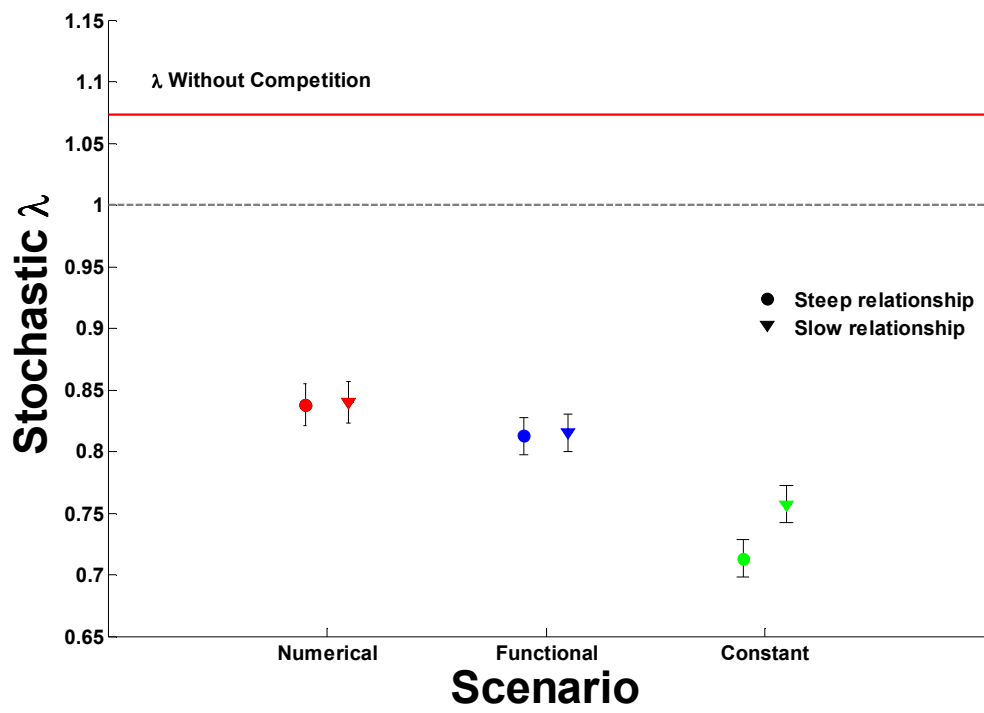
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541 Table 1.  
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Logistic functional relationships							
Vital rate	Age-class	Asymptotic value		Intercept		Slope	
		arctic	red	arctic	red	arctic	red
Prop. breeding	Adults	0.9	0.9	-4	-1	0.3	0.2
	Juveniles	0.4	0.4	-4	-0.09	0.2	0.1
Litter size	Adults	10.5	6.0	-5	-0.5	0.4	0.15
	Juveniles	5.5	3.0	-5	-0.05	0.35	0.15
Survival	Adults	0.7	0.7	-1	-1	0.35	0.3
	Juveniles	0.6	0.6	-2	-0.2	0.3	0.2
Inverse logistic function							
Type of response		Asymptote		Half Saturation Constant		Scaling Parameter	
Steep		0.40		50		7	
Slow		0.40		50		14	

- 548 1. Equation for the logistic functional relationships:  $asymptotic\ value / (1 + \exp(-[intercept + slope * (rodent\ density)]))$ .  
 549 2. Equation for inverse logistic relationship:  $1 - (asymptote / (1 + \exp(-[(red\ fox\ abundance - half\ sat) / scaling])))$ .

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