Paper IV
Strength of asymmetric competition between predators in food webs ruled by fluctuating prey: The case of foxes in tundra

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Abstract

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

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

The temporal dynamics of northern terrestrial food webs is often ruled by pronounced multi-annual population cycles of key herbivores like snow shoe hares or small rodents (voles and lemming) (Elton 1942). These herbivores represent key prey for guilds of vertebrate predators (Ims and Fuglei 2005, Korpimäki and Krebs 1996). The various predator species within these guilds may, however, differ somewhat in terms of the degree of specialization on habitat and prey, which in turn affects their numerical and functional
responses (Andersson and Erlinge 1977, Gilg et al. 2003, Krebs et al. 2001, Wiklund et al. 1999). Consequently, an evaluation of the outcome of asymmetric competition in such a system must consider the underlying prey dynamics as well as the competing predators’ numerical and functional responses to the prey cycle. For instance, if the dominant predator species operates as a typical resident specialist (cf. Andersson and Erlinge 1977), and responds numerically to the prey cycle (i.e. with a time-delay), the largest effect on subdominant competitors could be expected in the crash phase of the prey cycle. On the other hand, if the dominant species responds like a generalist that functionally shifts habitat and/or diet to track peak prey density populations, the greatest effect on the subdominant species could be expected in the increase and peak phases of the cycle. However, while the phases of the prey cycle with the most intense competition for different numerical and functional responses of the dominant predator may be rather straightforward to deduce, the outcome in terms of long-term viability of the subdominant species, and thus the likelihood for species co-existence within guilds, is in need of more elaborate analysis. In this study we provide such an analysis by means of modelling. We use a pair of interacting fox species in tundra ecosystems as a specific case. The analytical framework may, however, apply more broadly to competitive interactions between predators depending on strongly fluctuating prey populations.

As with other closely related canids (Clark et al. 2005, Fedriani et al. 2000, Nelson et al. 2007, Switalski 2003), competition between arctic fox (*Vulpes lagopus*) and red fox (*Vulpes vulpes*) can be expected to be fierce. Indeed, many studies have indicated that the larger sized red fox can expel the arctic fox in cases where their distribution range comes to overlap (Chirkova 1968, Killengreen et al. 2007, Linnell et al. 1999, Tannerfeldt et al. 2002). The importance of competition between the two fox species has been particularly emphasized in Fennoscandia where the decline of the arctic fox to near extinction, at least partly, have
been attributed to the expansion of the red fox into the mountain tundra (Kaikusalo and Angerbjörn 1995, Killengreen et al. 2007, Tannerfeldt et al. 2002). However, similar replacement of the arctic fox, by the red fox, appears to take place in many other places in the circumpolar tundra (Chirkova 1968, Hersteinsson and Macdonald 1992, MacPherson 1964, Marsh 1938).

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

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

**Modelling framework**

The general framework of our modelling consists of three interlinked compartments (Fig. 1). The first model compartment provides realizations of small rodent prey dynamics that phenomenologically simulate the characteristics (i.e. cycle period and amplitude) of typical vole and lemming cycles (Stenseth 1999). The two other compartments model the dynamics of the two fox species (Fig. 1). The arctic fox dynamics is always modelled as a resident
specialist with a pronounced numerical response (i.e. population dynamics) that is entirely
driven by the amount of available rodent prey (Angerbjörn et al. 1999). In this case, the arctic
fox population exhibits cycles with a typical one-year time lag relative to the prey cycle. The
red fox dynamics varies, however, among the three ecological scenarios considered. The first
scenario may apply to a setting in which large tracts of tundra is located far from adjacent
ecosystems. In this case the red fox (like the arctic fox) possesses the dynamical attributes of
a resident specialist (Englund 1970). We term this the numerical response scenario. In the
second scenario, we assume that the red fox has access to an alternative nearby habitat (e.g.
boreal forest) which is more profitable than tundra in terms of alternative prey resources in
the low phase of the rodent cycle. In the late increase and peak phase of the rodent cycle,
however, the red fox performs functional habitat switching (cf. Mysterud and Ims 1998) in
the sense that it invades the nearby tundra (Elmhagen 2003). In this scenario, which we term
the functional response scenario, the red fox has a cyclic abundance dynamics in tundra
similar to the numerical response scenario, but with the exception that the response to rodent
dynamics will be instant (i.e. direct prey tracking; cf. Korpimäki 1994) and not delayed with
a one-year time lag. In the third and final scenario we assume a stable red fox population in
tundra owing to some external food subsidy: i.e. the constant subsidy scenario. Likely
candidates for such subsidies are overabundant semi-domestic reindeer populations providing
carcass resources (Ims et al. 2007) or subsidies from marine food webs in coastal tundra
(Roth 2003).

For all scenarios we assume that red fox impacts population growth in arctic fox
through interference competition by which the red fox excludes the arctic fox from the most
2002). As a consequence the red fox affects the population growth rate of the arctic fox by
reducing the amount of prey available to the arctic fox. This reduction of available prey, and
resultant negative impact on arctic fox growth rate, increases proportionally with the prevailing abundance of red fox.

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

In the case of the functional response scenario, red fox abundance was simulated by using the time series generated from the numerical response scenario, but shifted one year as to obtain the non-delayed response (i.e. direct prey tracking). Thus, the functional and numerical response scenarios differ only in terms of the timing of the peak of red fox abundance and impact on arctic fox population growth. Finally, the stable red fox abundance
of the constant subsidy scenario was set equal to the mean abundance generated for the two other dynamic scenarios.

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

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

**Results**

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

The assumed proportional reduction of small rodent prey available to arctic fox, owing to interference competition with red fox (Fig. 2, Table 1), gave a substantial decrease in the long-term population growth rate ($\lambda$) of the arctic fox in all scenarios (i.e. compare the
estimated λ for the three red fox scenarios with the estimate without competition in Fig. 3). However more interestingly, the outcome of the three scenarios differed substantially. The strongest impact of competition was obtained in the scenario where a stable abundance of red fox was present in tundra (i.e. the constant subsidy scenario), whereas the weakest impact was seen when the red fox displayed the numerical response typical of a resident specialist predator (Fig. 3). The scenario in which the red fox displayed a functional shift in habitat, according to the prevailing small rodent density in tundra, gave an intermediate impact compared to the two other scenarios.

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

Discussion

We have documented that strongly asymmetric interference competition between species exploiting a cyclically fluctuating resource can yield different likelihoods of long-term persistence of the subordinate competitor, depending on the ecological context modifying the population dynamics of the dominant competitor. Although we have used two fox species belonging to tundra food webs ruled by cyclically fluctuating rodent populations as the case study for the model analysis, our predictions may apply to other predator guilds in similar ecological contexts. Below we first discuss the assumptions made regarding the performance
of the competing predators and the different ecological settings and scenarios explored. Then, we turn to the predictions derived from the modelling and their implications.

Assumptions

Predators typically differ in the degree of specialization on prey, ranging from obligatory specialists to full generalists (Andersson and Erlinge 1977). In food webs ruled by cyclic population dynamics of key herbivores, such as small rodents or snow shoe hares, some predators can act as facultative specialists (Roth et al. 2007) or actual specialists (Elmhagen 2003). This means that they specialize on the cyclic herbivore in regions where such cycles prevail, whereas they act as generalists in other regions and ecological settings. Both fox species considered in this study are facultative specialists. The red fox is an extremely versatile predator that inhabits a wide range of habitats, ecosystems and biomes, and thereby preys on whatever available in the various settings (Macdonald 2000). The arctic fox is restricted to the tundra biome, but can rely on alternative prey items to small rodents (e.g. marine subsidies) whenever such alternative resource are more available (Macdonald 2000). However, the most common setting for arctic fox populations, in the vast circumpolar tundra zone, is the one in which they depend on cyclic rodent populations. In that case, their population dynamics show the typical signature of a small rodent specialist; i.e. cyclic fluctuations lagging one year behind their prey (Angerbjörn et al. 1999, Ims and Fuglei 2005). Similar dynamics have been reported for the red fox in northern regions (Butler 1951, Elton 1942, Henden et al. 2008), thus verifying that both fox species may act as specialist predators according to our numerical response scenario. Moreover, as entire guilds of predators have been shown to respond synchronously to both small rodents (Pitelka et al. 1955) and snow shoe hares (Krebs et al. 2001), this scenario may apply to several other competing predators as well.
Owing to its wide habitat spectrum and diverse food web affiliations, we outlined an alternative functional response scenario for red fox in tundra. In this scenario, which is likely to apply to contexts where more productive and stable food webs are situated nearby tundra, a direct tracking of rodent peaks on the tundra is possible for a predator capable of performing habitat shifts. Although less empirical information is available for such “migration mediated dynamics” in the red fox, Butler (1951) suggested events of influx of red fox into the arctic tundra from adjacent boreal forest in Canada. In Fennoscandian mountain tundra, which is normally imbedded in large tracts of boreal forest, a similar non-delayed response to lemming peaks in red fox has become evident from efforts made to remove red fox from mountain tundra in the Swedish-Finnish arctic fox conservation programme (SEFALO 2004, Angerbjörn and Hellström, unpublished data). More generally, our functional response scenario applies to the response of nomadic specialist predators (usually very mobile avian predators) capable of rapid tracking of cyclic peaks of prey in time and space (Ims and Steen 1990).

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

In lack of detailed information on the dynamics of interference competition in the different scenarios, we assumed the same phenomenological outcome of asymmetric competition in all scenarios; namely a proportional reduction of available prey and
demographic performance of the arctic fox with increasing red fox abundance. Although
certainly more is to be learned about the mechanisms of competition between the two fox
species from future field studies, we think the assumed impact of competition on the
subdominant predator is essentially realistic if the dominant predator tends to occupy the
most resource rich patches in tundra. Current knowledge about the distribution of red and
arctic foxes, both in low arctic tundra (Killengreen et al. 2007) and mountain tundra (Dalén et
al. 2004, Elmhagen 2003, Frafjord 2003), is in line with the assumption that the red fox
occupies and expels the arctic fox from the most productive parts of the tundra. For instance,
lowland tundra harbours higher rodent densities than high altitude areas, particularly, in peak
years of voles not accompanied by lemmings (Ekerholm et al. 2001).

Predictions and implications

Our modelling framework yielded the prediction that different temporal dynamics of the
competitively dominants predator (albeit with the same temporal mean abundance) will give
contrasting long-term stochastic growth rate of the subdominant predator. In the two
scenarios with the same cyclic fluctuations of red fox abundance, the arctic fox performed
worse in the functional response than in the numerical response scenario. This means that the
timing of the maximum impact of competition matters. Specifically, maximum impact in the
peak phase of the prey cycle (the functional response scenario) has a larger effect on arctic
fox long-term growth rate than maximum impact in the crash phase (the numerical response
scenario). This kind of phase-dependence has an analogy in the field of life history theory,
where the reproductive value of cohorts has been shown to differ between different cycle
phases in cyclically fluctuating populations (Schaffer and Tamarin 1973, Stearns 1976).
By far the largest impact of competition was found in the scenario when the dynamics of the dominant predator was stabilized owing to an external subsidy. We think that this effect mainly stems from how the stabilization of red fox abundance affected the mean and variance of available prey to the arctic fox. Indeed, Henden et al. (2008) found that arctic fox long-term growth rate was sensitive to the temporal mean and the variance in the prey dynamics. In particular, the combination of decreased variance and mean abundance of rodents affects the stochastic growth rate of the arctic fox most negatively. Accordingly, in the present model the constant subsidy scenario yielded a lower mean (9.8 rodents/ha) and standard deviation (7.1) of available prey (i.e. when corrected for the reduction imposed by red fox competition) than the other scenarios. Such an effect is also likely to underlie the difference between the two dynamic response scenarios, as the numerical response had a higher mean (11.8) and standard deviation (10.1) than the functional response scenario (mean=10.9, SD=8.5).

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

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

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References:


Fuglei, E. and Ims, R. A. 2008. Global warming and effects on the arctic fox. - Science Progress 91:


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

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

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

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

A) Small rodents

- Numerical response
- Functional response
- Constant subsidy

B) Red fox

C) Arctic fox

% reduction

Numerical response

<table>
<thead>
<tr>
<th>Species</th>
<th>Density [Ind/ha]</th>
<th>Growth rate [λ]</th>
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<td>Arctic fox</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red fox</td>
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Fig. 2.
Fig. 3.

<table>
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Stochastic λ

- Steep relationship
- Slow relationship

Scenario

- Numerical
- Functional
- Constant
**Logistic functional relationships**

<table>
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<tr>
<th>Vital rate</th>
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<th>Intercept</th>
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<td>red</td>
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<td>red</td>
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**Inverse logistic function**

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<th>Asymptote</th>
<th>Half Saturation Constant</th>
<th>Scaling Parameter</th>
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<tbody>
<tr>
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<tr>
<td>Slow</td>
<td>0.40</td>
<td>50</td>
<td>14</td>
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</tbody>
</table>

1. **Equation for the logistic functional relationships:** \[ \text{asymptotic value} / (1 + \exp (- [\text{intercept} + \text{slope} \times \text{rodent density}])). \]

2. **Equation for inverse logistic relationship:** \[ 1 - (\text{asymptote} / (1 + \exp (- [\text{red fox abundance} - \text{half sat} / \text{scaling}])). \]