Title: Rabbits killing hares: an invasive mammal modifies native predator–prey dynamics

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Abstract

Invasive species management requires practical evidence of the impacts of introduced species over ecosystem structure and functioning. Theoretical ecology and empirical data support the potential of introduced mammals to drive native species to extinction, indeed the majority of practical evidence comes from insular environments, where conditions may differ from the mainland. We analyzed the effects of an introduced lagomorph, the eastern cottontail *Sylvilagus floridanus* on two native mammals, the European hare *Lepus europaeus* and the red fox *Vulpes vulpes*. We used relative abundances collected over 8 years at 30 protected areas in Italy. A generalized linear mixed model was fit to test various hypotheses about the relationships between cottontails, foxes and climatic conditions over the abundance of native hares. In our model, hare and cottontail abundances did not show a negative relationship and we believe that no direct competition occurs between the two species. However, the relationship between fox and hare abundances, positive when cottontails were

scarce, became more and more negative as cottontails increased: this supports the hypothesis that indirect dynamics like apparent competition exists between the two lagomorphs. Climatic conditions, expressed through the North Atlantic Oscillation, did not affect the relationship between cottontail and hare abundances. As the impact of parasites on mammal populations is generally climate dependent, we believe that cottontails do not play a direct role in the cycle of parasites affecting hares. Our results provide a clue that an invasive mammal, the eastern cottontail, is modifying the predator–prey relationship between two native species in a non-insular environment. The existence of such dynamics should lead wildlife managers to account for the effect of introduced species in their decision making, directing control activities on cottontails and not on native foxes.

Introduction

Introduced species are considered one of the main drivers of biodiversity loss (Kumschick et al., 2015) and their spread and impacts are likely to increase in an increasingly connected world (Hulme, 2009). The introduction of species changes the composition and functionality of ecosystems, and can drive native species to extinction through different mechanisms, such as predation, competition or diseases transmission (Bellard, Genovesi & Jeschke, 2016).

Interspecific competition operates primarily on individuals,with a reduction in their fitness; these effects will be translated at the population level, negatively influencing demographic parameters and possibly determining the decline or even the local extinction of one of the two species (Gurnell et al., 2004). The competitive process could be the results of interference or exploitation competition. Interference competition involves direct interactions between species, while exploitation competition implies indirect negative interactions arising from the use of a common resource (Schoener, 1983; Lang & Benbow, 2013). Traditionally, ecologists demonstrated the occurrence of competition with removal experiments that, however, are difficult to perform

(Schoener, 1983). Alternatively, data on demographic patterns (Forsyth & Hickling, 1998) and on species distributions (Bertolino et al., 2014) can be assessed for evidence of competition by examining whether the presence of one species negatively influences the population demography and the distribution of the other. However, competitive interactions may be more complex. Species that do not interact directly and do not exploit the same resources can still influence each other if they share common natural enemies, such as predators, parasites, or pathogens (Zhang, Fan & Kuang, 2006). For example, the so-called 'apparent competition' occur as an indirect effect when species that do not directly compete for resources affect each other by being prey for the same predator (Courchamp, Langlais & Sugihara, 2000; Noonburg & Byers, 2005; Gibson, 2006; Lang & Benbow, 2013). Competition, either direct or indirect, between introduced and native mammals has been found to occur on various contexts. Direct competitive interactions has been observed between introduced and native squirrels in Europe (Gurnell et al., 2004), as well as between marsupial and eutherian carnivores in Australia (Glen & Dickman, 2008). Apparent competition is another major consequence of introduced mammals, especially on islands when both a prey and a predator are introduced causing hyperpredation processes (Courchamp et al., 2000; Zhang et al., 2006). Other forms of indirect competition between native and invasive species include those mediated by diseases (Fournier-Chambrillon et al., 2004; Bruemmer et al., 2010; Strauss, White & Boots, 2012), whose transmission can be regulated by climatic conditions (Kiesecker, Blaustein & Belden, 2001; Beard & O'Neill, 2005; Skerratt et al., 2007). As the various competitive dynamics arising with the introduction of invasive mammals can produce long-standing effects on ecosystems, assessing their structure and magnitude is crucial to design effective policies aimed at reducing the impact of invasive species meanwhile minimizing collateral damage to ecosystems (Bergstrom et al., 2009).

This work aims at modeling the ecological impact of an invasive mammal in northern Italy. Notably, we would like to test the occurrence of competitive processes with a native species, as well as the occurrence of apparent competition. The eastern cottontail *Sylvilagus floridanus* has been

introduced in north-western Italy during the 1960s and it is now widespread in northern and central Italy (Bertolino, Ingegno & Girardello, 2011b; Bertolino et al., 2011c). Its interactions with the native European hare *Lepus europaeus* are complex, because the two species select different macro- and microhabitats (Bertolino, Cordero di Montezemolo & Perrone, 2011a, 2013; Vidus-Rosin et al., 2011), but cottontails carry several viruses and parasites, which can potentially affect hares (Bertolino et al., 2010; Tizzani et al., 2011, 2014; Zanet et al., 2013; Lavazza et al., 2015). Finally, the red fox *Vulpes vulpes*, a major predator for hares in Europe (e.g. Lindström et al., 1994; Reynolds & Tapper, 1995), includes cottontails in its diet when they are available (Balestrieri, Remonti & Prigioni, 2006).

To the best of our knowledge, no study has examined the population dynamics of hares, cottontails and foxes in areas where all these species coexist. Nevertheless, we deem such an approach necessary to fully address the issue of potential impacts of introduced cottontails. Particularly, we tested three hypothesis based on previous knowledge about the potential impact of invasive cottontails on native hares in Italy.

In the first hypothesis (H_1), we theorized that invasive cottontails and native hares are direct competitors for environmental resources. Previous works do not provide evidence for this, however, they analyzed a limited geographical scale (Bertolino et al., 2011a, 2013) and had a cross-sectional design (Vidus-Rosin et al., 2011) that we deemed poor in revealing complex biotic interactions, compared to large-scale data and time series (Wisz et al., 2013). As a consequence of H_1, we expected that a negative, clear correlation occurred between cottontail and hare abundances.

In the second hypothesis (H_2), we predicted that cottontails play a role in the transmission of parasitic diseases to native hares. Parasites and some infective diseases (e.g. pseudotuberculosis) have a higher impact on hare populations in cold and wet years (Chroust, 1984; Wibbelt & Frölich, 2005). Therefore, we expected that the abundance of cottontails had a negative correlation with the abundance of hares and that such correlation was stronger in wet and cold years, when body

conditions of hare worsen and there is a higher number of parasites at the infective stage in the environment (Stromberg, 1997).

In the third hypothesis (H₃), we hypothesized that cottontails negatively affect hares through indirect competition, modifying their relationships with foxes. In this case, we expected that the magnitude of the correlation between hare and fox abundances changed at different levels of cottontail abundance.

Materials and Methods

Study areas and data collection

The study area was located in the lowlands of the province of Torino (Piedmont, Italy), where the wildlife office every year monitors small game at 30 protected areas through spotlight counts (Fig. 1). From December to January, gamekeepers carry out three spotlight census from an off-road vehicle on fixed transects, recording hares, foxes and cottontails. We used the 2008–2015 data, expressing the relative abundance of each species as the number of individuals per kilometer of transect (kilometric index of abundance, KIA), and averaging abundances for every year. Despite a lively debate about the effectiveness of relative indexes to model ecological dynamics (Anderson, 2001; Engeman, 2003), we deemed the KIA a reliable measure of population abundance, because we conducted longitudinal data analysis and because of its wide adoption in studies about the population ecology of lagomorphs and small carnivores (Gortazar et al., 2007; Sobrino et al., 2009; Barrio, Acevedo & Tortosa, 2010; Preatoni et al., 2012).

Climatic data

Climatic conditions were expressed as winter (January–March) and summer (July–September) averages of the North Atlantic Oscillation (NAO; Lamb & Peppler, 1987) The NAO accounts for

multiple climatic factors influencing many ecological dynamics in Europe and affecting the ecology of endothermic organisms, like mammals (Ottersen et al., 2001; Schmidt, Asferg & Forchhammer, 2004; Straile & Stenseth, 2007; Gordo, Barriocanal & Robson, 2011). Because our study area was close to the Mediterranean, where the effects of the NAO have been less studied than in central Europe, before using the NAO as a covariate in our model, we decided to test its associations with seasonal temperatures and rainfalls. We downloaded monthly values of the NAO from http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml and data about temperatures, rainfalls and moisture for the city of Torino from http://archivio-meteo.distile.it/. Associations between winter/summer NAO and local climate were always linear, and significant Pearson's correlations are shown in Table 1.

Statistical analysis

As a first step to investigate a possible direct competition between the two lagomorphs, we evaluated the Pearson's correlation coefficients between KIAs of hares and cottontails in the 2008–2015 period for each area.

Then, we modeled the effect of cottontails, foxes and weather covariates on hare abundance with a generalized linear mixed model with a Gamma distribution of the error, a random intercept and a log-link. The random structure of the model was selected on the basis of the lowest value of the Akaike's information criterion (Zuur et al., 2009). The choice of a Gamma distribution of the error was made by observing the distribution of the response variable, which was non-normal (Shapiro test: $W = 0.77$, $P < 0.01$) and positively skewed (2.46). Since no distance-dependent pattern emerged in trends correlations, we decided to discard spatial explicit modeling. Weather covariates included winter NAO, as a measure of winter and summer conditions, and summer NAO, due to its correlation with spring weather. Winter weather was included in the model because harsh conditions

can lead to higher energy needs of hares, reducing their body conditions (Hackländer, Arnold & Ruf, 2002a), making them more susceptible to diseases (Smith, Vaughan Jennings & Harris, 2005) and reducing the milk production during the breeding season (Hackländer, Tataruch & Ruf, 2002b). Winter NAO index also accounted for summer conditions from July to September, when hare densities are at their maximum and density-dependent factors like coccides (Chroust, 1984) can operate. Spring weather was included in the model as it affects the survival of leverets by acting on thermoregulation (Hackländer et al., 2002a). We also added an interaction between winter and summer NAO indexes, to account for inter-seasonal effects of weather conditions. Two other inter-action terms were included to the model. The first one accounted for an interaction between cottontail abundance and winter NAO, representing our second hypothesis about the role of cottontails in disease transmission and their interactions with winter and summer conditions. The second interaction term accounted for an interaction between cottontail and fox abundances and expressed our third hypothesis of indirect competition.

Collinearity of predictors was checked by graphical exploration of correlations and with the variance inflation factors. Predictors were not multicollinear and all of them were included in the initial model. As they were on different scales, predictors were standardized. Furthermore, graphical exploration of their relationships with the response variable enabled us to exclude higher order interactions. The set of predictors was selected with the information criteria approach, starting from the beyond optimal model (Zuur et al., 2009). Once we identified the best model, residuals were plotted for evaluating the fixed term and to eventually detect patterns. We also graphically explored the normality of random effects. We estimated Nakagawa's R^2 to measure the proportion of data variability explained by the model (Nakagawa & Schielzeth, 2013). Statistics were computed with R (R Development Core Team 2015).

Results

We could not find any clear pattern in the temporal trend of local abundances of hares and cottontails (see Supporting Information Fig. S1). A significant correlation was found only in six out of 30 sampled areas: five correlations were positive with r = 0.74–0.97 and only one negative with r = 0.72 (all p < 0.05, see Supporting Information Table S1).

Residuals of GLMM did not show any clear pattern (see Supporting Information Fig. S2) and normality of the random effects was respected (see Supporting Information Fig. S3). Despite the fixed-term of the model accounted for a small proportion of the total variability of the data (marginal $R^2 = 0.15$), the whole model with the random term explained a good proportion of the variability in the data (conditional $R^2 = 0.73$).

Cottontail abundance was positively and significantly correlated to hare abundance (β = 0.19 ± 0.04, p < 0.01), and the same applied for fox and hare abundances (β = 0.75 ± 0.21, p < 0.01) (Table 2). However, the interaction term between cottontail and fox abundances was negative and significant (β = 0.16 ± 0.05, p < 0.01), therefore the relationship between hares and foxes changed as cottontail abundance increased. The KIA of foxes was positively associated to the KIA of hares, in conditions of scarce cottontails (β = 0.67 ± 0.19, for 0.55 cottontails/km), while the relationship between foxes and hares was increasingly negative at increasing cottontail abundances (β = 0.04 ± 0.15, for 5 cottontails/km; b = 0.82 ± 0.33, for 10 cottontails/km) (Fig. 2). From our model (Table 2), winter values of the NAO index were negatively associated to hare abundance (β = 0.43 ± 0.13, p < 0.01), but their interaction with cottontail abundance was not significant and had a low marginal effect (β = 0.03 ± 0.02, p = 0.09). The interaction term between summer and winter values of the NAO was significantly and negatively associated to hare abundance (β = 0.36 ± 0.09, p < 0.01).

Discussion

The spatial–temporal data analysis on the population dynamics of native hares and introduced cottontails does not support our first hypothesis about a direct interference between these two

species. The local abundances of the two species were generally not correlated and, even when, the correlation was positive in five out of six cases. Also considering the areas altogether with a GLMM model, cottontails do not seem to be direct competitors of hares, as the correlation between the two species was positive. Instead, hares and cottontails seem to covary: this could mean that the two species are subjected to similar limiting factors, like summer rainfalls (Jacobs & Dixon, 1981; Hackländer et al., 2002a,b; Smith et al., 2005; Rödel & Dekker, 2012).

On the other hand, our data supported the third hypothesis, with evidence of an impact of invasive cottontails on prey–predator dynamics of native hares and foxes. The relationship between foxes and hares, positive when cottontails are scarce, becomes strongly negative when cottontails increase their numbers. An initial positive correlation between foxes and hares in the presence of few or no cottontails, indicate that their population dynamics are more influenced by external factors, for example, habitat quality (Bertolino et al., 2011c), than by species interactions. Furthermore, we believe that two non-exclusive hypotheses can be advanced to explain the pattern we observed when cottontails increase.

In the first hypothesis, an increase in cottontail abundance would lead to a numerical response of foxes, magnifying their predatory impact on hares. This dynamic is known as 'hyperpredation' and it is a particular case of apparent competition, a well-known impact of alien mammals that can produce profound changes in the relationship between native prey and predators (Norbury, 2001; Oliver, Luque-Larena & Lambin, 2009) and in the trophic interactions between native species (Roemer et al., 2001). In hyperpredation, an introduced prey species, easy to kill and predation resilient, triggers the extinction of a native prey species by rapidly increasing the population size of their predators (Courchamp et al., 2000). Despite invasive, species are often suboptimal preys for native predators compared to native species; they can become important supplemental food resources, contributing to boost up predator populations (Pintor & Byers, 2015). In turn, such an increase in the abundance of native predators affects native preys, as increased predation pressure

can have a densityindependent and prolonged impact on their populations (Noonburg & Byers, 2005). Hyperpredation can be an overwhelming force for those native species who do not have very high growth rates or suitable behavioral anti-predator response (Courchamp et al., 2000), driving them to collapse. In our case, we deem cottontails matching all the requirements for triggering hyperpredation of foxes on native hares. The reproductive rate of cottontails is high and can make their population resilient to prolonged and intensive predation by foxes (Balestrieri et al., 2006), while native hares do not have high growth rates and may not be able to cope with high densities of foxes in intensive agricultural landscapes (Panek, 2009), like those in the study area.

In the second hypothesis, cottontails would trigger a case of 'spillover' predation by foxes on native hares, around patches of permanent cover. Spillover predation occurs when predators emigrate from one source habitat where they find a primary prey, and they start foraging in sink habitats where they can find secondary preys (DeCesare et al., 2010). Various field studies indicate that spillover predation is relatively common among generalist predators and that it can seriously affect prey populations occurring in proximity of permanent sources of food (Kristan & Boarman, 2003; Oro & Martínez-Abraín, 2007; Sanz-Aguilar et al., 2009). In our case, we believe that cottontails can become a main prey for foxes in the study area, because of their limited home range and the constant selection of permanent cover that can make them predictable preys (Swihart, 1986; Bertolino et al., 2013). Therefore, foxes would alter their foraging behavior, choosing permanent patches of vegetation rich of profitable preys. As these habitats are also important resting sites for adult and young hares (Fernex, Nagel & Weber, 2011; Neumann et al., 2012), an increased presence of foraging foxes is likely to result in a higher predation risk for hares.

These two hypotheses are not mutually exclusive and future studies, based on diet analysis and radiotracking, may properly quantify them. As indirect competition between mammal species often produces time-delayed impacts (Hansen et al., 1999), time series analysis could also be another fruitful approach to disentangle interactions between cottontails, hares and foxes.

The lack of any interaction between cottontail abundance and the winter NAO on hare abundances partly rejects our second hypothesis about a significant role of cottontails as reservoirs for disease impacting hares. Cottontails are unlikely to play a clear role in the cycle of parasites like coccides, reaching their infestation peak on hares in autumn and whose abundance is strongly affected by climatic conditions (Chroust, 1984). If cottontail had influenced coccide loads of hares, the sign and magnitude of their relationship with hare abundance would have changed strongly with different climatic conditions. On the other hand, we cannot be completely sure about the lack of any role of cottontails in the transmission of other diseases, whose dynamics are less related to seasonal conditions. For example, cottontails can also be infected by EBHSV (Lavazza et al., 2015), and the same applies to foxes eating infected lagomorphs (Chiari et al., 2016). We recommend future studies exploring the potential role of cottontails in the epidemiology of EBHSV, as this virus is a serious threat for hare populations in Europe (Chiari et al., 2014).

Our model also provides valuable insights about the impact of climatic conditions on hare abundance. Hares seem to be scarcer in years with a positive winter NAO, characterized not only by mild and dry winters but also by rainy summers. This is contrary to previous studies on the effect of winter weather (Schmidt et al., 2004) but in line with evidence about the detrimental effect of summer rains (Hackländer et al., 2002a,b; Smith et al., 2005; Rödel & Dekker, 2012). The interaction between winter and summer NAO was significant and part of the best set of predictors, suggesting that wet springs can magnify the negative effects of adverse weather in winter and/or summer, by decreasing the survival of leverets (Hackländer et al., 2002a).

In this study, we provided evidence for an indirect effect of introduced cottontails on native hares through apparent competition. We conducted longitudinal data analysis on the abundance of the three species, while previous studies were cross-sectional and did not consider indirect interactions with foxes, failing in finding any impact (Bertolino et al., 2011a, 2013; Vidus-Rosin et al., 2011). We therefore highlight the need to use adequate data, with spatial replicate and temporal trends, to

test hypotheses about the interactions between native and introduced species (Ricciardi et al., 2013). When an invasive species becomes widespread, it is important to evaluate possible impacts in the new ecosystems and considering its trophic interactions with new species, as these two tasks are crucial for policy making and environmental management. In fact, obtaining adequate or upgraded information about the ecological impact of biological invaders, lays the foundation for their classification and their inclusion in black lists (Blackburn et al., 2014; Hawkins et al., 2015). Furthermore, knowing the interaction between native and invasive species is mandatory to design effective eradication campaigns or numerical control schemes, without unintended consequences (Zavaleta, Hobbs & Mooney, 2001).

As we found support for apparent competition between invasive cottontails and native hares, our research challenges some game management activities that are common in northern Italy. Foxes are considered a main predator of hares, a possible negative effect of predation on hare populations was suggested, though other studies did not support this view (Lindström et al., 1994; Reynolds & Tapper, 1995; Smith et al., 2005). Despite this disagreement between studies and the need of local evidences on the relationship between hares and foxes, irregular predator control is a common measure in Italy, as it is believed to increase game population densities, including hares. Previous research on invasive mammals has demonstrated that invasive prey species should be managed by keeping them at a low level of abundance through a constant culling effort, avoiding periodic shifts in their abundance, which exacerbates the impact of predators on native preys (Norbury, 2001). This is exactly the opposite of the approach of wildlife managers to introduced cottontails, whose densities fluctuate throughout the year due to the hunting season or the poor implementation of local voluntary control schemes. The existence of trophic interactions between cottontails and native foxes should discourage wildlife managers from adopting irregular culling schemes for these two species. We believe that numerical control of foxes is unlikely to be effective to restore hare populations in the study area, because it is far from reaching the enforcement standards that are

required for a serious impact on fox populations (Mahon, 2009) and because abundant cottontails can enable rapid recovery of fox populations. Similarly, we believe that carrying out irregular numerical control of cottontails, without a constant effort, may negatively affect native species without preventing a future recovery of cottontail populations. We suggest that a data-informed game management activity should be focused on a regular control of cottontail populations, and we encourage future human dimensions research aimed at designing the most effective control strategy (Santo et al., 2015).

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Figures

Figure 1. Study area and the network of protected areas around the city of Torino where species were sampled.
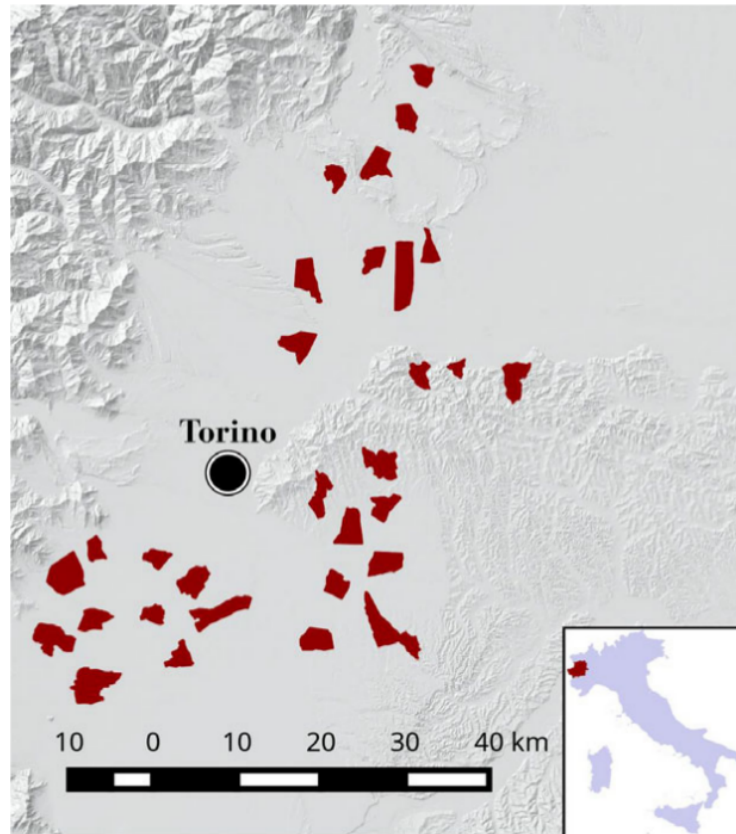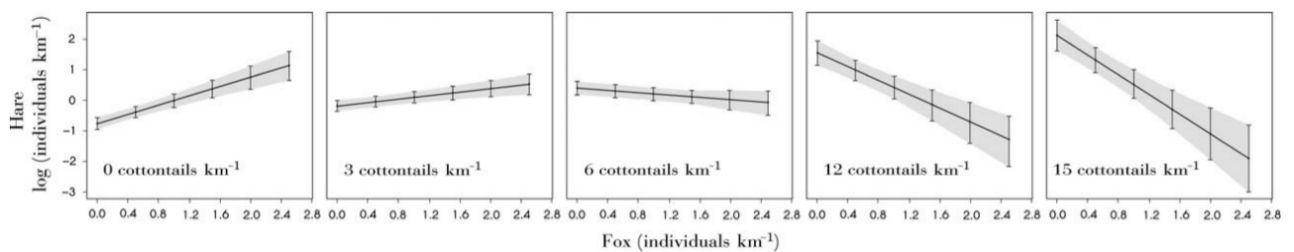

Figure 2. Effect of foxes on hare abundance, at different levels of cottontail abundance; hares data are log-transformed.

Tables

Table 1. Significant Pearson's correlations between North Atlantic Oscillation (NAO) and local climate.

		Pearson's correlation	
NAO index	Local climate	Coefficient (r)	p-value
Winter (Jan - Mar)	Winter temperature (°C)	0.79	p < 0.01
	Winter rainfalls (mm)	-0.52	p < 0.01
	Winter moisture (%)	-0.64	p < 0.01
Summer (Jul - Sept)	Summer rainfalls (mm)	0.51	p < 0.01
	Summer temperature (°C)	-0.30	p < 0.01
	Summer rainfalls (mm)	0.02	p < 0.01
	Spring temperature (°C)	-0.57	p < 0.01
	Spring rainfalls (mm)	0.70	p < 0.01

Table 2. Generalized linear mixed model output

	Coefficients	Standard error	t	p
Fixed effects				
Intercept	-0.80480	0.20251	-3.974	0.00007
Cottontail	0.18755	0.03623	5.177	0.0000002
Fox	0.75206	0.21159	3.554	0.000379
Summer NAO	-0.12221	0.07370	-1.658	0.097280
Winter NAO	-0.43381	0.12672	-3.423	0.000618
Cottontail X Fox	-0.15720	0.04586	-3.428	0.000602
Cottontail X Winter NAO	0.02711	0.01597	1.698	0.089553
Winter NAO X Summer NAO	-0.36104	0.09847	-3.667	0.000246
	Variance		Standard deviation	
Random effects				
Intercept (site)	0.3331		0.5772	
Residual	0.3112		0.5579	

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Model indexes				
AIC = 299.1	BIC = 332.0	LogLik = -139.6	Deviance = 279.1	Residual = 289
NAO, Norh Atlantic Oscillation; AIC, Akaike's Informative Criterion; BIC, Bayesian Informative Criterion				