The wolves of Isle Royale display scale-invariant satiation and ratio-dependent predation on moose

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Summary

1. The importance of two features of the predator functional response (satiation and predator dependence) is investigated in the wolf–moose interaction on Isle Royale National Park (Michigan, USA). This is done by fitting and comparing nine different functional response models to the observed kill rates.

2. Three different observational scales (the whole island, the wolf packs, or a 'mixed' scale) are used to assess the sensitivity of the detected properties with respect to these spatial scales.

3. Independently of the observational scale and of statistical assumptions on data structure, strong predator dependence and satiation of the wolf functional response are found. The 'mixed' scale gives the most consistent results, suggesting that predation should be measured for each pack, but that packs share all moose on the island. On this scale, the functional response is clearly ratio-dependent.

Key-words: *Alces alces*, *Canis lupus*, functional response, predator interference, scale invariance

Introduction

To understand the functioning of natural predator–prey systems, one often uses simple mathematical models. A key element in these models is the functional response (number of prey eaten per predator per unit of time). Different mathematical forms of the functional response can alter significantly the predictions of these models (Arditi & Berryman 1991; Arditi, Ginzburg & Akçakaya 1991; Ginzburg & Akçakaya 1992; Yodzis 1994; Wood & Thomas 1999). Precise information about the functional response in natural predator–prey communities is therefore a key element to understand the dynamics of these populations.

The well-known Isle Royale National Park (Michigan, USA) presents a case where prey (moose *Alces alces* L.)

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and predators (wolves *Canis lupus* L.) have been coexisting in a single-prey/single-predator system for over 50 years. These populations have never been hunted by humans, and their dynamics have been closely monitored since 1959. Moreover, counts of moose kills are available since 1971.

In the frequent cases in which predator and prey abundance time series are available without the kill numbers, the functional response must be inferred indirectly by statistical techniques that suffer inevitable uncertainties (Carpenter, Cottingham & Stow 1994; Jost & Arditi 2000, 2001; Jost & Ellner 2000). Direct measurements of the functional response in field conditions are very rare and involve complicated methodologies in order to manipulate both prey and predator abundances and to estimate the predation rate (Schenk, Bersier & Bacher 2005). The Isle Royale system is exceptional because it provides the necessary data to assess the functional response directly and in unmanipulated field conditions.

In a recent paper, Vucetich, Peterson & Schaefer (2002) compared these data with several functional response models. They found that the model that greatly outperformed the others was the type 2

ratio-dependent model (as introduced by Arditi & Ginzburg 1989 and analysed by Jost, Arino & Arditi 1999 and by Berezovskaya, Karev & Arditi 2001). This model is a function of the moose–wolf ratio and displays satiation for high ratios. The other models included in particular the more traditional prey-dependent functional responses, which are functions of moose density only.

A ratio-dependent functional response is the manifestation of strong density dependence among predators [also called predator dependence, see Arditi *et al.* (2004) for a deeper discussion] such as intraspecific competition for resources or direct interference (Arditi & Akçakaya 1990; Akçakaya, Arditi & Ginzburg 1995; Arditi *et al.* 2004). Ratio-dependent and prey-dependent models make very different predictions about the stability of the system and the control mechanisms at work (bottom-up vs. top-down control, see Arditi & Ginzburg 1989; Arditi *et al.* 1991; Ginzburg & Akçakaya 1992; Abrams & Ginzburg 2000; Ponsard, Arditi & Jost 2000).

Vucetich *et al.* (2002) measured predation success for each wolf pack separately and computed the functional response (i.e. kills per wolf per unit time) in each pack. This dependent variable was then modelled as a function of total wolf and moose density on Isle Royale. The analysis was thus conducted on a 'mixed scale', that is, the dependent variable was measured on a per pack scale while the independent variables were measured on the scale of the whole island. However, it may also be sensible to consider a 'whole island' scale only, with both dependent and independent variables measured on the whole island. Alternatively, one could work on a 'per pack' scale, with wolf density, moose density, and the functional response measured for each pack and its territory. A priori, it is difficult to know whether any of these approaches is biologically more appropriate than the others.

In this paper, we will analyse all three scales with the purpose of detecting general features of wolf predation that are scale-independent, paying particular attention to the two features of density dependence and satiation. This will be done by model selection for which we will use a bootstrap technique (model-based nonparametric resampling, Davison & Hinkley 1997) rather than the information criterion approach employed by Vucetich *et al.* (2002). The latter is more appropriate for selecting predictive models than for hypothesis testing (Burnham & Anderson 1998, p. 132), which is the purpose of the present work. In order to reduce the risk of overseeing the most appropriate model, we also select among nine different functional responses.

The data

Isle Royale is 544 km[2] in area and situated 24 km from the northern shore of Lake Superior (North America). Moose arrived on Isle Royale at the beginning of the twentieth century, while wolves arrived only in the late 1940s. Because the winter diet of wolves consists of ≈ 90% moose (Thurber & Peterson 1993) and the latter have no other predators than wolves, this system represents a relatively simple predator–prey system (unlike most other wolf populations in North America or Europe that are embedded in a multipredator and multiprey system, Jedrzejewski *et al.* 2002). The study of these populations was initiated in 1959 and continues to the present. Here, we will analyse the data from 1971 (when estimates of kill rate started) to 1998.

During this period, wolf and moose abundances, moose kills and the wolf's social organization in packs have been estimated annually (during January and February) by aerial survey (see Vucetich *et al.* (2002) for details).

These data permit us to analyse the system on three levels/scales that emphasize different aspects of the spatial and social organization of moose and wolves:
1. *Per pack scale*. Kills per wolf per day (calculated in each pack) studied in relation to pack size and moose abundance per pack territory (85 values of the kill rate, wolf abundance and moose abundance).
2. *Whole island scale*. Kills per wolf per day (computed over the whole island) as a function of total wolf and moose populations (28 values of the kill rate, wolf abundance and moose abundance).
3. *Mixed scale*. Kills per wolf per day in each pack, but studied as a function of total wolf and moose populations (85 values of the kill rate, 28 values of wolf abundance and moose abundance).

The 'per pack' scale considers each pack with its territory and the moose therein as an independent unit, but it ignores interactions among packs and the overlapping of territories. The 'whole island' scale represents the aggregated population level that avoids any spatial or social details. The 'mixed' scale finally tries to combine both views to account for both the wolf's social structure and the free movement of moose on the island.

Methods

The functional response *g* (kills per predator per unit time) is by definition an instantaneous rate (Solomon 1949). Traditionally, the most general theories of *g* assume that it may be influenced by both prey (N) and predator (P) abundances, i.e. $g(N,P,\theta)$ (with $\theta = (\theta_1, \theta_2, \dots)$ the parameters of the model). Given measurements of prey, predator and the kill rate k_{obs} (in our case the total number of kills per day divided by the number of wolves), estimating goodness-of-fit and the parameters for a particular form of *g* becomes a standard nonlinear regression problem. We will use the least squares method to solve it:

$$e = \min_{\theta} \sum_{k_{obs}} (k_{obs} - g(N,P,\theta))^2. \qquad \text{eqn 1}$$

Note that eqn 1 used in the context of information criteria (as in Vucetich *et al.* 2002) assumes the uncertainties in k_{obs} to be Gaussian while they are more likely to be

Table 1. The analysed functional response models and their properties: satiation ($\max_{(N,P)} g(\cdot) < \infty$), predator dependence ($\partial g/\partial P < 0$). A + or – indicates presence or absence of these properties

$g(N,P,\theta)$	Name	Group	Satiation	Predator dependence
a	Cst	a	+	–
$aN/(1 + ahN)$	Ho2	a	+	–
aN	LV	a,b	–	–
$\alpha(N/P)$	RD1	b	–	+
$\alpha(N/P^m)$	HV1	b	–	+
$\alpha N/(P + \alpha hN)$	RD2	c	+	+
$\alpha N/(P^m + \alpha hN)$	HV2	c	+	+
$aN/(1 + ahN + cP)$	DAB	c	+	+
$aN/[(1 + ahN)(1 + cP)]$	CM	c	+	+

Poissonian. However, a preliminary analysis (Devulder 2000) showed that assuming a Poisson error does not change the results. A more important issue is that actual observations are never instantaneous and that, during the observation time, the prey abundance declines due to loss by predation. Thus the quantity k_{obs} defined above is not an instantaneous rate, as it should be. Denoting by Na the total number of kills, T the total observation time and N_0 the prey abundance at time 0, the functional response is linked to this total number of kills by the formula

$$\int_{N_0}^{N_0 - N_a} \frac{dN}{g(N,P,\theta)} = -\int_0^T P \, dt.$$

Solving this equation will in general lead to an expression that is implicit in the total kill Na (Royama 1971; Rogers 1972; Arditi & Akçakaya 1990). For given parameters θ, it must be solved numerically ($Na(N,P,T,\theta)$) and the regression with this integrated response becomes:

$$e_I = \min_\theta \sum_{k_{obs}} \left(k_{obs} - \frac{Na(N,P,T,\theta)}{P} \right)^2 \qquad \text{eqn 2}$$

Standard software packages cannot solve this problem or only with additional programming (Arditi & Akçakaya 1990; Juliano 1993). For this reason, one often tries to avoid these complicated computations by assuming that prey abundance does not change during the observation period. The actual prey losses on Isle Royale during the observations were at most 5%, a value that can be considered negligible compared with other errors in the data. However, to make sure that the results are independent of this simplification we will analyse the data in both ways, interpreting the estimated predation rates either as instantaneous or as integrated responses.

The coding is done in C++, solving the implicit equations by bisection and the minimization problem by the simplex method of Nelder–Mead combined with simulated annealing (Press *et al.* 1992).

THE FUNCTIONAL RESPONSE MODELS AND THE MODEL SELECTION SCHEME

Theory suggests that the functional response is: (a) an increasing and bounded function of available prey, and (b) independent of predator density or a decreasing function of this density. We will select among nine forms of the functional response with one, two or three parameters that incorporate these properties to varying degrees (see Table 1). The Cst (constant), LV (Lotka–Volterra) and Ho2 (Holling type 2) are standard functional response models that can be found in many textbooks with the underlying mechanistic reasonings (e.g. Begon, Mortimer & Thompson 1996). RD1 and RD2 are a linear and a type 2 (bounded) ratio-dependent functional response that were shown to emerge on a global scale from local LV interactions, the essential ingredients being spatial or temporal heterogeneities that lead to predator aggregations and prey refuges (Michalski *et al.* 1997; Poggiale, Michalski & Arditi 1998; Cosner *et al.* 1999; Arditi *et al.* 2001; Vucetich *et al.* 2002). HV1 and HV2 are a linear and a type 2 form of the Hassell–Varley type (Hassell & Varley 1969) that consider the attack rate a in LV and Ho2 to be a decreasing function of predator density, modelled empirically by $a = \alpha P^{-m}$. Finally, DAB is the DeAngelis–Beddington functional response (Beddington 1975; DeAngelis, Goldstein & O'Neill 1975) that assumes that predator individuals either search, consume or interfere with each other. CM is a variation of DAB that assumes that interference precedes consumption (Crowley & Martin 1989). We will not analyse sigmoid functional responses because the wolves on Isle Royale have no other prey to which they could switch.

As we want to detect the importance of predator dependence and satiation in wolf predation we will classify these models in three groups: (a) models without predator dependence (LV, Cst, Ho2); (b) models without satiation (LV, RD1, HV1); and (c) models containing both features (RD2, DAB, CM, HV2). Within each group the best fitting model will be determined by goodness-of-fit (eqn 1) and the significance of differences between models of different complexities (i.e. with different numbers of parameters) will be assessed by model-based nonparametric resampling (Davison & Hinkley 1997) described below. Finally, the selected models from each group will be ordered by their goodness-of-fit and the significance of their differences will be determined by the same resampling method in order to make a final selection of the best-fitting model.

Table 2. Parameter estimates for the selected functional responses for each scale (fitted values ± bootstrapped α-trimmed standard error with α = 0·05). On the left for the instantaneous functional response (eqn 1), on the right for the integrated functional response (eqn 2)

	Instantaneous	Integrated
Per pack (HV2)	$e = 0.0124$	$e_I = 0.0124$
α [day^{-1}]	0.0127 ± 0.0186	0.0132 ± 0.0224
h [day]	24.1 ± 1.94	24.2 ± 1.96
m	1.85 ± 0.32	1.85 ± 0.35
Whole island (RD2)	$e = 0.0010$	$e_I = 0.0010$
α	0.00067 ± 0.00019	0.00069 ± 0.00021
h	17.2 ± 4.4	17.5 ± 5.9
Mixed scale (RD2)	$e = 0.0116$	$e_I = 0.0116$
α	0.00110 ± 0.00016	0.00112 ± 0.00027
h	16.4 ± 2.2	16.5 ± 2.4

BOOTSTRAP METHODS FOR PARAMETER ESTIMATION AND MODEL SELECTION

Standard errors of the fitted parameters will be estimated by the standard nonparametric bootstrap method described in Efron & Tibshirani (1993, p. 47) with 1000 bootstrap samples.

Model selection will be done with model-based nonparametric resampling (Davison & Hinkley 1997; Jost & Ellner 2000) and least-squares (eqn 1). In this method, models are compared one to one to test the null-hypothesis (H_0) that the data were produced by the model that fits worse and the better-fitting model does so only by chance. To do this, we create bootstrap samples by taking the worse-fitting model and randomizing the residuals (with replacement). Then we fit again each pair of models to the bootstrap sample. This method estimates the empirical distribution of the difference in goodness-of-fit between the two models under H_0, which can then be compared with the original difference. The proportion of bootstrapped differences that were greater than the original difference is an estimate of the smallest P-value for which the difference is significant. We consider H_0 rejected if $P < 0.05$.

Results

Table 2 reports the error and parameter values with both error functions e (eqn 1, instantaneous) and e_I (eqn 2, integrated) for the best fitting models (see below). We note that they are almost the same. As the model selection procedure also gives the same results with both error functions (Devulder 2000) we will only report the details of the analysis with the instantaneous functional response.

The results of the bootstrap selection procedure are summarized in Table 3. For selecting within groups, the comparisons between models of different complexity are rated with the usual stars (*, ** and *** for $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively). The models selected within each group are noted on the last line and the results of one-to-one comparison

Table 3. Model selection results: the first column contains the models (ordered by goodness-of-fit), the second column their number of parameters (np), the third the error (e, eqn 1), and the remaining three columns the results of the comparisons within each model group (a: without predator dependence, b: without satiation, c: models with both properties). The line 'Selected model' contains the model selected for each group, while the following lines contain the results of the comparisons between these winners. The finally selected model is in bold face type

Per pack scale

model	np	e	group a	group b	group c
RD1	1	0·0724			
LV	1	0·0402			
HV1	2	0·0402			
Cst	1	0·0186			
Ho2	2	0·0170			
RD2	2	0·0132			
DAB	3	0·0132			
CM	3	0·0125			
HV2	3	**0·0124**			
Selected model			Ho2	LV	**HV2**

Whole island scale

model	np	e	group a	group b	group c
Cst	1	0·00276			
RD1	1	0·00188			
LV	1	0·00176			
Ho2	2	0·00175			
HV1	2	0·00135			
RD2	2	**0·00101**			
DAB	3	0·00101			
HV2	3	0·00101			
CM	3	$9.88 \cdot 10^{-4}$			
Selected model			LV	HV1	**RD2**

Mixed scale

model	np	e	group a	group b	group c
RD1	1	0·0191			
Cst	1	0·0186			
LV	1	0·0165			
HV1	2	0·0155			
Ho2	2	0·0152			
RD2	2	**0·0116**			
HV2	3	0·0116			
DAB	3	0·0116			
CM	3	0·0113			
Selected model			Ho2	HV	**RD2**

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; NS, non-significant.

(in increasing order of goodness-of-fit) are also rated with stars. The finally selected model is marked in bold face type for each scale.

Let us first look at the best fitting model in each group of models. Among the models without predator dependence (group a), the Ho2 model fits significantly best for the 'per pack' scale and the 'mixed' scale, while for the 'island' scale Ho2 does not fit significantly better than LV despite its additional parameter. Among the models without satiation (group b) LV is selected for the 'per pack' scale while HV1 fits significantly
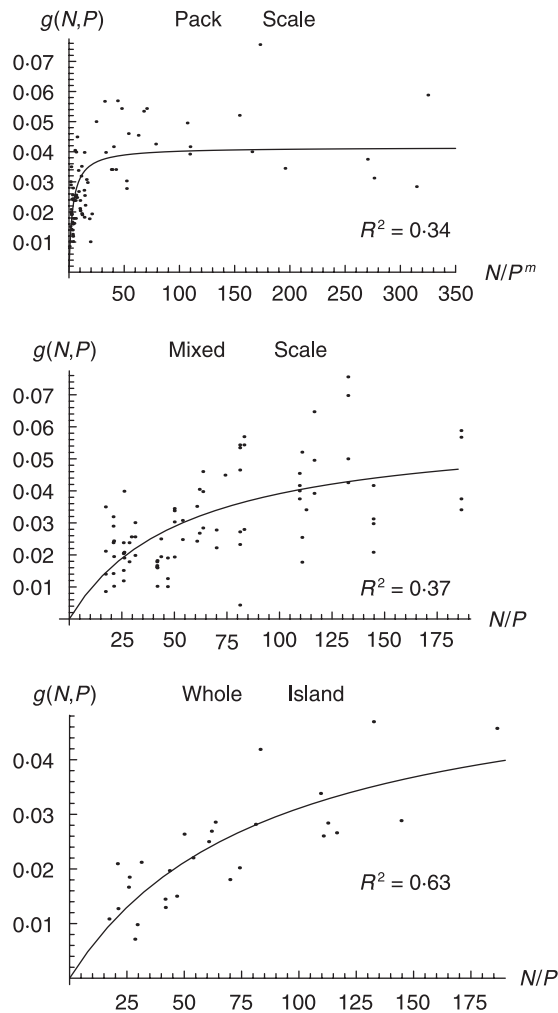
Fig. 1. Fits of the finally selected models (with the corresponding coefficients of determination R^2): the Hassell–Varley type 2 model for the 'per pack' data, the ratio-dependent type 2 model for the 'mixed scale' data and for the 'whole island' data. The data on the 'mixed scale' correspond to those analysed in Vucetich *et al.* (2002).

better for the 'whole island' and 'mixed' scales. Finally, among the 'full' models (group c), HV2 wins significantly for the 'per pack' scale, while RD2 is selected on the 'whole island' and 'mixed' scales.

Comparing now the best fitting models between groups we note that the selected model always belongs to the third group (with satiation and predator dependence): the HV2 model is selected for the 'per pack' scale, while RD2 is selected on the 'mixed' and the 'island' scales. The fitted functional response curves are shown in Fig. 1 for these winning models, together with the observed values.

The estimated parameters of the winning models are reported in Table 2. The handling time h is quite independent of the scale and the estimates of 16–24 days seem somewhat high but still plausible (Thurber & Peterson 1993). The parameter α varies over one order of magnitude. This parameter is therefore very scale-dependent.

Discussion

From a statistical point of view, the data on the scale of the 'whole island' and on the 'mixed' scale are well described by the simplest functional response that has both predator dependence and satiation (ratio-dependent type 2 fits significantly best compared with the other tested functions). The 'per pack' data have a more complex predator dependence, with the Hassell–Varley type 2 model fitting best (significantly). These results suggest unambiguously that the rate of wolf predation on Isle Royale depends importantly on wolf density and displays satiation effects, independently of the chosen scale.

This analysis has emphasized the spatial scale, but the time scale may also be important. This can be explored with the 'whole island' data. By taking moving averages of all variables over two, three, or more years, one mimics different observation time scales (Ginzburg & Colyvan 2004). Figure 3 shows the results of fitting three equally complex models to such data: Ho2 (satiation, no predator dependence), HV1 (no satiation, predator dependence) and RD2 (both satiation and predator dependence). The prey-dependent model Ho2 is clearly outperformed by both predator-dependent models RD2 and HV1. Note that for small window sizes, satiation (in RD2) is of strong importance, while for larger window sizes it is rather the modulation of predator dependence (P^m in the denominator of HV1) that slightly increases model fit. It is also interesting to note that model fits reach maximal values with a window size of ≈ 6 years (with the generation time of wolves about 4 and moose about 9).

The HV2 model contains both Ho2 and RD2 as special cases for $m = 0$ (Ho2, prey-dependent) and $m = 1$ (RD2, ratio-dependent). For this reason model selection is often done by constructing confidence intervals of the parameter m and testing the hypotheses $m = 0$ or $m = 1$ [see Arditi & Akçakaya (1990), Stow, Carpenter & Cottingham (1995), or Skalski & Gilliam (2001)]. As the model HV2 leads to overfitting on the 'mixed' and 'whole island' scales, we have preferred here a different model selection technique based on the goodness-of-fit of the model given the data (Jost & Ellner 2000; Jost & Arditi 2001). Nevertheless, it is of interest to study the uncertainty of the estimates of m. Figure 2 shows the bootstrapped distributions of this parameter on the three scales: they all show a rather wide distribution of m, all very different from $m = 0$, while $m = 1$ seems a reasonable approximation for the 'whole island' and 'mixed' scale. On the 'per pack' scale, m is clearly greater than 1. Such high values of m have occasionally been reported in field studies of various systems (Hassell 1978, 2000; Sutherland 1996; Ponsard *et al.* 2000; Jost & Arditi 2001) but they are puzzling because $m > 1$ indicates overcompensating interference: the whole wolf pack captures less moose as the pack size increases. We do not want to speculate here about possible mechanisms for this effect, which
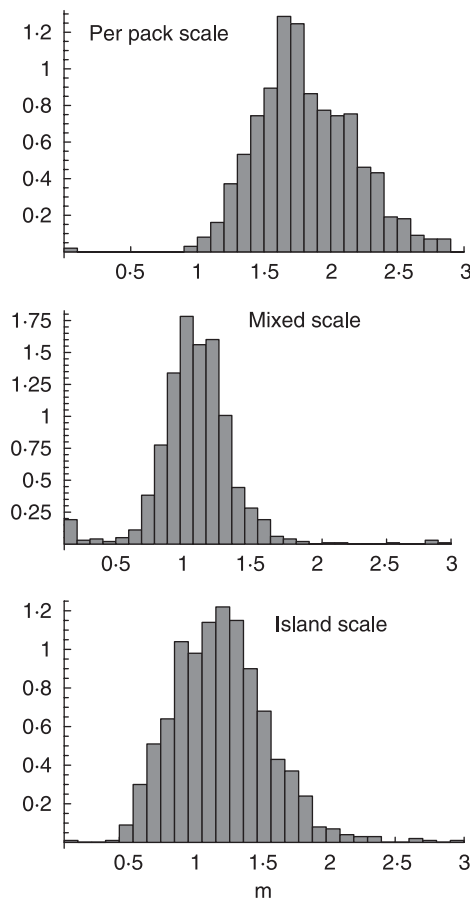
Fig. 2. Empirical distributions of the mutual interference parameter *m* of the Hassell–Varley type 2 model, computed with a nonparametric bootstrap, for the 'per pack', 'mixed' and 'whole island' scales.

only appears on the 'per pack' scale. As will be discussed below, the 'mixed' scale appears to be more reasonable.

The major result is the clear evidence (irrespective of the scale of analysis) of strong predator dependence. The underlying biological reasons will need further study. It will be difficult, if not impossible, to disentangle all mechanisms that are at work: social structure within packs, competition within packs, competition between packs, partial prey consumption, etc. Because many mechanisms are at work, fitting models that include only one mechanism at a time will only tell whether this particular mechanism can help explaining the observed pattern, but little about its importance compared with the other additional mechanisms. For this reason, we do not see a problem in using an empirical model such as HV2.

Another important feature of the functional response is satiation (i.e. an asymptotic approach to a maximum kill rate): the nonsaturated but predator-dependent Hassell–Varley type I model fits worse than the equally complex saturated Ho2 or RD2 models. Only with long moving averages on the 'whole island' scale does HV1 fit slightly better than RD2 (Fig. 3). A limitation of the HV1 model is that it cannot generate population cycles, which may be a feature of the
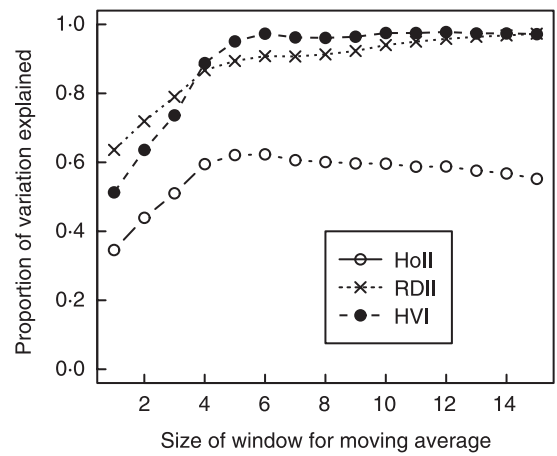
Fig. 3. R^2 (proportion of variation explained) for the three two-parameter models Ho2, RD2 and HV1 as a function of the size of the moving average window over the dependent and independent variables (see also fig. 5·1 in Ginzburg & Colyvan 2004).

wolf–moose dynamics on Isle Royale (Post *et al.* 2002; but see Vucetich & Peterson 2004). Specifically, the HV1 model cannot produce limit cycles in a standard model with logistic prey growth and constant predator mortality rate (Jost 1998). Neither satiation nor predator dependence alone can explain the data satisfactorily. The RD2 or HV2 models win because they have both characteristics.

This study was undertaken to perform model selection for a given data set, but not to choose which scale is the most reasonable biologically. However, as the 'per pack' and 'mixed' scales have the same number of data points, we can compare them directly. Several aspects speak in favour of the 'mixed' scale: (a) it has always slightly better goodness-of-fit measures in Table 3; (b) its residual structure in Fig. 1 looks more reasonable; and (c) the high value of *m* on the 'per pack' scale is difficult to explain with biological or theoretical arguments.

To summarize, we have identified satiation and predator dependence to be essential ingredients of wolf predation across several scales. Thus, they should be part of any dynamic model developed for this population. The ratio-dependent model is a good approximation on the 'mixed' and the 'whole island' scales and only on the 'per pack' scale does a more complex model such as the Hassell–Varley type 2 model perform better. However, as just said, the 'per pack' scale has several shortcomings. Although the detection of satiation is not very surprising, the detection of strong predator interference is quite interesting and confirms previous evidence available in diverse natural and artificial systems.

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