An Adaptive Intraguild Predation Model for Drought- and Disease-Triggered Lynx Predation on Black Kites

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ABSTRACT

A discrete-time, stage-structured intraguild predation model is developed to examine why Iberian lynx began taking black kite nestlings in Doñana only after the rabbit collapse associated with RHDV2 and during droughts. The model couples a rabbit resource, a drought-sensitive fallback, and an intake-dependent lynx diet switch to kite recruitment and little owl abundance. A reference simulation reproduces the observed conditional onset of nest predation and the direction of the demographic cascade. Fitting the diet switch to 25 annual nest-count observations gives an AIC of 554.3, compared with 557.5 for an interacting rabbit-density–drought logistic model. The data constrain the location of a sharp rabbit-density transition only to 0.32–1.34 rabbits per hectare. Substituting observed duck counts for the drought fallback worsens fit, leaving the identity of the drought-dependent mechanism unresolved. These results support a behavioral switching mechanism as a sufficient, but not unique, explanation of the observed pattern.

KEYWORDS adaptive foraging • intraguild predation • drought • RHDV2 • Iberian lynx • black kite

1 Purpose and scope

This document describes a discrete-time, stage-structured intraguild predation (IGP) model built to test whether a single foraging mechanism can reproduce the empirical pattern reported by Sergio et al. (2026) for the Doñana National Park, Spain: Iberian lynx (*Lynx pardinus*) began killing black kite (*Milvus migrans*) nestlings only after rabbit haemorrhagic disease virus type 2 (RHDV2) collapsed the shared rabbit prey base, and only in drought years, with predation rising steeply once rabbit density fell below roughly one rabbit per hectare. Lynx predation lowered kite lifetime reproductive success and abundance, and lower kite abundance was associated with higher abundance of the little owl (*Athene noctua*), a prey of adult kites.

The model is used in two ways. Sections 3 to 8 treat it as a sufficiency test: with parameters set by hand to published summary quantities, it asks whether the observed drought × prey-scarcity interaction, the density threshold, the lagged kite response and the owl cascade follow from one assumption, that lynx add kite nestlings to their diet only when intake from preferred prey falls below a threshold, as predicted by optimal diet theory (Charnov 1976; Stephens and Krebs 1986). The empirical quantities used for that calibration, such as the drought years, the timing and size of the rabbit crash, the range of kite pair numbers and the approximate density threshold, are taken from the published study. Everything else is a modelling choice. Section 9 turns the diet-switch component into a fitted statistical model: it is driven by the observed rabbit and drought series, fitted to the annual nest counts by maximum likelihood, and compared by AIC with the generalized linear model used in the article. The demographic and cascade components are not fitted; their agreement with the data is checked qualitatively.

The study is framed in terms of intraguild predation (Polis et al. 1989; Holt and Polis 1997), a body of theory that descends directly from the Lotka–Volterra predator–prey equations (Lotka 1925; Volterra 1926). The canonical IGP model

of Holt and Polis (1997) is a three-species Lotka–Volterra system with linear functional responses. The empirical paper therefore sits inside the Lotka–Volterra lineage even though it does not use the name. Section 6 writes out the Holt–Polis system and explains why a model with constant interaction coefficients cannot reproduce the observed on/off switching, which motivates the adaptive-foraging extension developed here.

2 The empirical system being modelled

The following facts from Sergio et al. (2026) and associated reporting constrain the model.

- Study plot of about 10 km² in northern Doñana, holding a stable population of 4 to 6 adult lynx and between 105 and 223 black kite breeding pairs over 1993–2023; kites made up 82–90% of the local raptor assemblage.
- Rabbits were the dominant shared prey: up to 80% (mean 58%) of the kite diet and 70–99% of the lynx diet before the crash.
- RHDV2 reached the wild population in 2013 and local rabbit density fell by more than 70%.
- Drought years were defined from Landsat inundation maps as years in which the minimum flooded marsh area in February–March was below 20% of the 1975 maximum: 1993, 1999, 2005, 2012, 2016, 2018, 2019, 2022 and 2023.
- Lynx predation on kite nests was negligible before the crash and in wet years after it, and rose exponentially with declining rabbit density in drought years, taking off below about 1 rabbit per hectare. The analysis covered 1,624 nests over 25 years; 108 nests were attributed to lynx.
- Only well-feathered nestlings (about 40–45 days) were taken; no attacks on younger nestlings were recorded in more than 13,000 hours of nest photography.
- Adults whose broods were taken had lower lifetime reproductive success and abandoned or shifted territories more often the following season.
- Annual kite abundance was related to the previous year's lynx predation rate, and little owl abundance was negatively associated with kite abundance.
- In earlier rabbit shortages, lynx shifted to ducks and other waterbirds; drought dries most of the marsh and removes that fallback.

3 Model structure

The model runs on an annual time step t, matching the breeding-season census structure of the data. Lynx numbers are held constant because the field population was stable and territorial; the lynx enters the model through its diet choice rather than its numerical response. The state variables and drivers are listed in Table 1.

Table 1. State variables, drivers and derived quantities.

Symbol	Meaning	Units / range
R_t	Rabbit density, the shared basal resource	rabbits per ha
W_t	Availability of wetland fallback prey (waterbirds) to lynx	index, 0–1
N_t	Black kite breeding pairs (IG prey; nestlings are the vulnerable stage)	pairs on the 10 km² plot
O_t	Little owl abundance index (prey of adult kites)	index, scaled to carrying capacity 1
L	Adult lynx on the plot (IG predator), held constant	individuals
D_t	Drought indicator (exogenous driver)	0 or 1
I_t	Lynx intake from preferred prey	energy-equivalent index
p_t	Fraction of feathered kite broods taken by lynx	0–p_max
s_t	Probability a nest reaches the feathered stage	0–1
J_t	Kite fledglings produced in year t	individuals
Λ_t	Kite pairs that lost their brood to lynx	pairs
A_t	Surviving, non-dispersing adult pairs entering year t	pairs
Q_t	New pairs recruited from the cohort fledged three years earlier	pairs

Figure 1 summarizes the causal structure. Two exogenous shocks act on different parts of the lynx diet: the disease removes the primary prey and drought removes the fallback. The lynx diet switch converts their conjunction into predation on kite nestlings, which propagates to kite demography and from there to little owls.

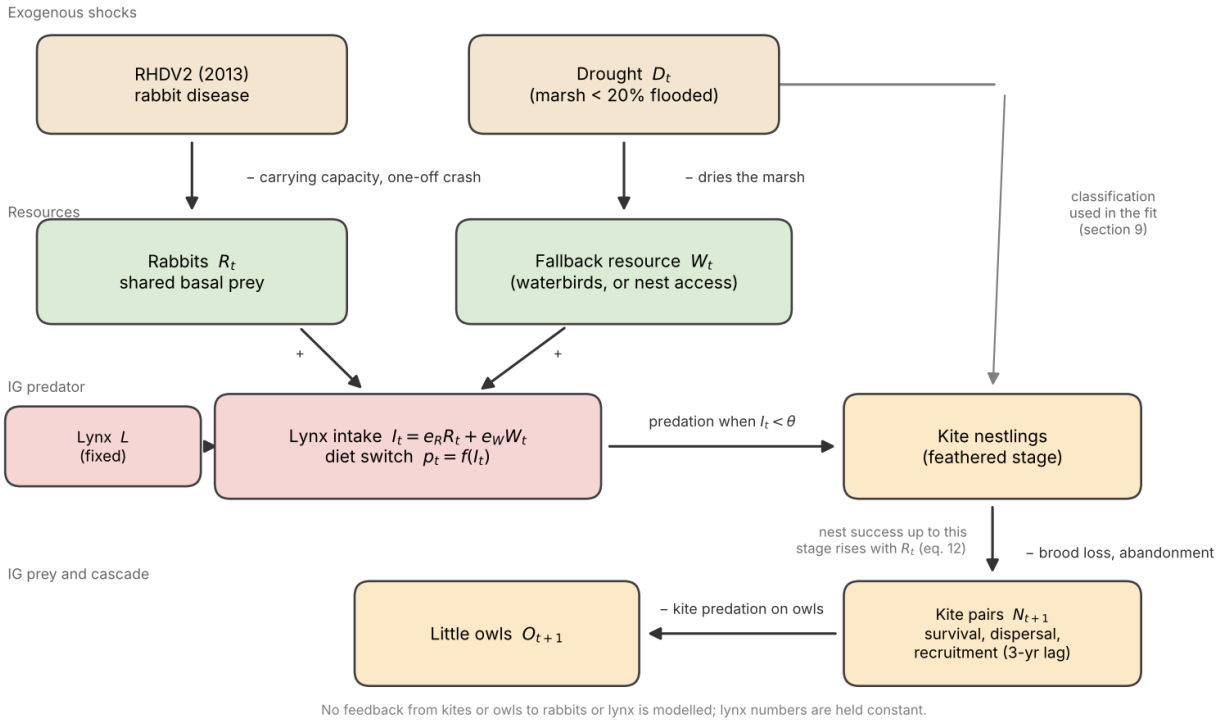


Figure 1. Causal structure of the model. Boxes are state variables or drivers; arrows are the dependencies written out in section 4, with the sign of each effect. The two exogenous shocks enter the lynx intake budget through different resources, and only their conjunction opens the diet switch. The grey link from drought to kite nestlings marks the binary classification used when the switch is fitted to the Source Data (section 9).

4 Equations

4.1 Exogenous drivers

Drought is a binary indicator derived from the inundation criterion of the empirical study, where $A_t^{\min}$ is the minimum flooded area in February–March of year t and $A^{\max}$ is the maximum flooded area recorded since 1975:

$$D_t = \begin{cases} 1, & A_t^{\min} < 0.2\, A^{\max}, \\ 0, & \text{otherwise}, \end{cases} \tag{1}$$

In the simulation D_t is read directly from the published list of drought years for 1993–2023. During the 40-year spin-up before 1993, drought years are drawn independently with probability 0.2, the empirical frequency in 1993–2012.

The rabbit disease acts through the rabbit carrying capacity and a one-off mortality in the arrival year t_c = 2013:

$$K_t = \begin{cases} K_{\text{pre}}, & t \le t_c, \\ K_{\text{post}}, & t > t_c, \end{cases} \tag{2}$$

4.2 Rabbits (shared basal resource)

Rabbits follow a stochastic Ricker model (Ricker 1954), chosen over the logistic because it stays positive under large perturbations and is the standard discrete-time analogue of logistic growth. Drought reduces the growth rate by a factor φ_D, representing the lower productivity of Mediterranean grasslands in dry years:

$$g_t = r_R\big[1 - (1 - \varphi_D)D_t\big] \tag{3}$$

$$R_{t+1} = R_t \exp\left[g_t\left(1 - \frac{R_t}{K_t}\right) + \varepsilon_{R,t}\right](1 - c)^{\mathbb{1}[t+1=t_c]} \tag{4}$$

where $\varepsilon_{R,t} \sim N\left(0,\ \sigma_R^2\right)$ is lognormal process noise, c is the one-off disease mortality fraction, and $\mathbb{1}[\cdot]$ is the indicator function, so the factor (1 − c) is applied once, in the transition into the arrival year. The carrying capacity used in that single transition is K_{pre}, so that the crash is not double-counted; from the following year the lower capacity K_{post} applies. Predation losses to lynx and kites are absorbed into the net growth rate rather than modelled explicitly, because at the field densities (4–6 lynx, 100–220 kite pairs on 1,000 ha) consumption is a small fraction of rabbit production and the published analysis treats rabbit density as a driver of the predators rather than the reverse. A floor of 0.02 rabbits per ha prevents numerical extinction.

4.3 Wetland fallback prey

The model needs a quantity that is removed by drought and that enters the lynx intake budget. The hypothesis adopted here is wetland fallback prey: lynx in earlier rabbit shortages switched to ducks and other waterbirds, and drought dries more than 80% of the marsh. The variable is therefore written as a waterbird availability index driven by drought:

$$W_t = \big[W_{\text{wet}}(1 - D_t) + W_{\text{dry}}D_t\big]\exp(\varepsilon_{W,t}) \tag{5}$$

with $\varepsilon_{W,t} \sim N\left(0,\ \sigma_W^2\right)$. Two cautions apply. First, the Source Data test in section 9.4 shows that the published duck counts do not explain the drought effect better than the drought indicator itself, so the identity of the fallback is not established; W should be read as "whatever drought removes from the lynx's options", which could also include access to the nest trees once the marsh beneath them is dry. Second, the model only requires that W be large in wet years and small in drought years; its exact values matter little once the switch is a step (section 9.3).

4.4 Lynx diet switch

Lynx intake from preferred prey is a linear combination of rabbit density and fallback availability, each weighted by an energetic conversion:

$$I_t = e_R R_t + e_W W_t \tag{6}$$

The fraction of feathered kite broods taken in year t is a decreasing sigmoid of intake. This is the only nonlinearity needed to reproduce the drought × scarcity interaction:

$$p_t = \frac{p_{\max}}{1 + \exp[k(I_t - \theta)]} \tag{7}$$

Here θ is the intake threshold below which kite nestlings become worth attacking, k controls the sharpness of the switch and $p_{\max}$ is the maximum annual predation rate, limited by the lynx's ability to locate and climb to nests. In the limit k $\longrightarrow \infty$ the switch becomes a step:

$$p_t \longrightarrow p_{\max} \mathbb{1}[I_t < \theta] \tag{8}$$

Derivation from optimal diet theory

Equation (7) is a smoothed version of the prey inclusion rule of the classical optimal diet model (Charnov 1976; Stephens and Krebs 1986). Let prey type j have energy value e_j, handling time h_j and encounter rate λ_j. A forager already taking rabbits (R) and waterbirds (W) should add kite nestlings (N) to its diet if and only if the profitability of nestlings exceeds the long-term intake rate from the current diet:

$$\frac{e_N}{h_N} > \frac{\lambda_R e_R + \lambda_W e_W}{1 + \lambda_R h_R + \lambda_W h_W} \tag{9}$$

The right-hand side is an increasing function of the encounter rates, which scale with R_t and W_t. Collapsing it to the linear index I_t and the left-hand side to the constant θ gives the step rule in equation (8). The zero-one form is a known feature of the optimal diet model: inclusion of a prey type does not depend on that prey's own abundance, only on the abundance of more profitable types. That is exactly what the field data show, since lynx attacks did not track kite density but switched on and off with rabbit and wetland availability. Křivan (2000) and Křivan and Diehl (2005) analyse this rule embedded in Lotka–Volterra IGP dynamics and show that adaptive omnivory of this kind generates abrupt diet shifts and widens coexistence relative to the fixed-diet Holt–Polis model. The sigmoid in equation (7) replaces the step with a smooth function to represent variation among individual lynx and within-year variation in prey availability.

Threshold rabbit densities

Setting $I_t = \theta$ gives the rabbit density at which the switch is half-open. In drought years:

$$R^*_{\text{dry}} = \frac{\theta - e_W W_{\text{dry}}}{e_R} \tag{10}$$

and in wet years:

$$R^*_{\text{wet}} = \frac{\theta - e_W W_{\text{wet}}}{e_R} \tag{11}$$

With the parameter values of Table 2, $R^*_{dry} \approx 0.94$ rabbits per ha, matching the empirical take-off point near 1 per ha, while $R^*_{wet} \approx -0.15$ is negative, so the switch cannot open in a wet year at any positive rabbit density. The interaction between drought and rabbit scarcity is therefore not an assumption of the model but a consequence of the fallback prey entering the same intake budget as rabbits.

4.5 Black kites

Kites are modelled as breeding pairs with a three-year pre-breeding delay, consistent with first breeding at three to four years in this species, and with lynx predation acting only on the feathered-nestling stage. This makes the model a stage-structured IGP system in the sense of Mylius et al. (2001) and Hin et al. (2011), where the IG predator consumes only one life stage of the IG prey.

Nest success up to the feathered stage depends on rabbit availability through a saturating function, with a floor α so that kites can still breed on alternative prey:

$$s_t = s_0 \left[\alpha + (1 - \alpha) \frac{R_t}{R_t + h} \right] \tag{12}$$

Fledglings produced in year t are the feathered broods that escape lynx predation, times the mean brood size f:

$$J_t = N_t s_t (1 - p_t) f \tag{13}$$

Pairs whose brood was taken by lynx:

$$\Lambda_t = N_t s_t p_t \tag{14}$$

Adult pairs entering the next season survive at rate σ_a and abandon the plot with probability d_0 if they kept their brood and d_p if they lost it to lynx. This is the mechanism through which the observed territory abandonment and dispersal after brood predation enter the model:

$$A_{t+1} = \sigma_a \big[(N_t - \Lambda_t)(1 - d_0) + \Lambda_t (1 - d_p) \big] \tag{15}$$

Recruits are fledglings from three years earlier that survived the pre-breeding period with probability σ_j, divided by two to convert individuals into pairs:

$$Q_{t+1} = \frac{\sigma_j}{2} J_{t-2} \tag{16}$$

Recruitment and immigration ι are limited by territory availability through a linear ceiling at K_N pairs, a Beverton–Holt-style density dependence acting on settlement rather than on survival (Beverton and Holt 1957):

$$N_{t+1} = A_{t+1} + \max\!\left(0, 1 - \frac{A_{t+1}}{K_N}\right) (Q_{t+1} + \iota) \tag{17}$$

Because predation enters N_{t+1} through Λ_t and dispersal, and enters N_{t+4} through the recruit cohort, the model produces the one-year lag between predation and kite abundance reported empirically, plus a weaker delayed echo.

4.6 Little owls (trophic cascade)

Little owls are a prey of adult kites. They follow a Ricker model with an added kite-dependent mortality term, scaled so that the mortality equals m_O at a reference kite density:

$$O_{t+1} = O_t \exp\!\left[r_O \left(1 - \frac{O_t}{K_O}\right) - m_O \frac{N_t}{N_{\text{ref}}} + \varepsilon_{O,t} \right] \tag{18}$$

This is the simplest representation of mesopredator release (Ritchie and Johnson 2009): a reduction in the intermediate predator relaxes mortality on its prey. Any mechanism that lowers kite numbers would produce the same owl response, so this component of the model is a consistency check rather than a discriminating test.

5 Parameters

Table 2 lists all parameters, the values used, and the basis for each. Values marked ”calibrated” were adjusted so that the simulated system reproduces quantities reported in the empirical study; values marked ”assumed” are plausible but unconstrained by the study and are the first candidates for sensitivity analysis.

Table 2. Parameter values used in the reference simulation.

Parameter	Value	Meaning	Basis
r_R	0.9	Rabbit intrinsic growth rate (per year)	Assumed; typical of European rabbit in Mediterranean habitat
K_{pre}	2.6 per ha	Rabbit carrying capacity before RHDV2	Calibrated so pre-crash density is well above 1 per ha
K_{post}	0.7 per ha	Rabbit carrying capacity after RHDV2	Calibrated to a > 70% decline
c	0.72	One-off mortality in 2013	Empirical: > 70% local decline
φ_D	0.75	Rabbit growth multiplier in drought	Assumed
σ_R	0.12	Rabbit process noise (SD, log scale)	Assumed
W_{wet}, W_{dry}	1.0, 0.05	Waterbird availability in wet and drought years	Calibrated; drought dries > 80% of marsh
σ_W	0.10	Waterbird noise (SD, log scale)	Assumed
L	5	Adult lynx on plot	Empirical: 4–6
e_R, e_W	1.0, 1.15	Intake weights of rabbits and waterbirds	Calibrated so wet years never open the switch
θ	1.0	Intake threshold for attacking nests	Calibrated to the ~1 rabbit per ha take-off
k	7	Switch steepness	Calibrated to the ”exponential” rise
$p_{\max}$	0.35	Maximum fraction of feathered broods taken	Calibrated; 108 of 1,624 nests over 25 yr, concentrated in 5 drought years
s_0	0.70	Base probability of reaching feathered stage	Assumed; typical black kite nest success
α	0.55	Floor of nest success when rabbits are absent	Assumed; kites take birds, fish, reptiles, crayfish
h	0.4 per ha	Half-saturation of rabbit effect on nest success	Assumed
f	1.9	Fledglings per successful nest	Assumed; typical of black kite
σ_j	0.50	Survival from fledging to first breeding (3 yr)	Assumed; consistent with raptor juvenile survival
σ_a	0.86	Adult annual survival	Assumed; consistent with black kite estimates
d_0	0.04	Baseline territory abandonment	Assumed
d_p	0.25	Abandonment after brood loss to lynx	Calibrated to ”more frequent” abandonment
K_N	250 pairs	Territory ceiling	Calibrated to the 105–223 range
ι	5 pairs per yr	Immigration	Assumed
r_O, K_O	0.6, 1.0	Little owl growth and capacity	Assumed; owl index is dimensionless
m_O, N_{ref}	0.5, 160	Kite-induced owl mortality at reference kite density	Assumed
σ_O	0.03	Owl process noise (SD, log scale)	Assumed

6 Relationship to Lotka–Volterra and Holt–Polis intraguild predation theory

The two-species Lotka–Volterra predator–prey system (Lotka 1925; Volterra 1926) for a prey X and predator Y is

$$\begin{aligned} \frac{\mathrm{d}X}{\mathrm{d}t} &= X(r - aY), \\ \frac{\mathrm{d}Y}{\mathrm{d}t} &= Y(baX - m), \end{aligned} \tag{19}$$

Holt and Polis (1997) extended this to a basal resource R, an intermediate consumer N (the IG prey) and a top consumer P (the IG predator) that eats both:

$$\frac{\mathrm{d}R}{\mathrm{d}t} = R\left[r\left(1 - \frac{R}{K}\right) - a_{RN}N - a_{RP}P\right] \tag{20}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = N\left[b_{RN}a_{RN}R - a_{NP}P - m_N\right] \tag{21}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = P\left[b_{RP}a_{RP}R + b_{NP}a_{NP}N - m_P\right] \tag{22}$$

Mapping to the Doñana system, R is rabbits, N is kites, P is lynx and a_{NP} is the lynx attack rate on kites. The central results of Holt and Polis are that coexistence requires the IG prey to be the superior competitor for the shared resource, and that along a productivity gradient the IG prey is favoured at low productivity and the IG predator at high productivity, with coexistence in between. These results hold with fixed attack rates.

Three properties of the fixed-coefficient model prevent it from reproducing the empirical findings. First, because the term $a_{NP}NP$ is bilinear with a constant coefficient, predation on kites is never zero while both species are present; the model cannot produce 20 years of negligible predation followed by discrete years of 25–30% nest loss. Second, the model has no variable other than R and N that could carry the drought effect, so the observed conditionality on drought has no place to enter. Third, the model has no stage structure, so it cannot represent predation confined to a 40–45-day nestling window, nor the delayed recruitment that produces the lagged kite response. The present model addresses the first two problems by replacing the constant a_{NP} with the state-dependent switch of equations (6)–(8), following the adaptive-omnivory extensions of Křivan (2000) and Křivan and Diehl (2005), and the third by moving to a discrete annual time step with explicit nestling and pre-breeding stages, following Mylius et al. (2001) and Hin et al. (2011).

A further simplification relative to Holt–Polis is that lynx numbers are fixed. In the full system the lynx would have a numerical response to rabbits, and the rabbit crash would reduce lynx density, which could weaken or delay the predation effect. Holding L constant is consistent with the field observation of a stable territorial population over the study period and keeps the comparison between the two mechanisms clean, but it is the first extension to test.

7 Simulation protocol

- Time steps: annual, 1993–2023, preceded by a 40-year spin-up with pre-crash rabbit capacity and randomly drawn drought years so that 1993 begins at the pre-crash steady state.
- Forcing: the published drought years and the 2013 RHDV2 arrival are imposed as described in section 4.1; nothing else varies systematically between years.
- Noise: lognormal process noise on rabbits, waterbirds and owls, with fixed seeds for reproducibility (NumPy default_rng).
- Reference run: seed 7, used for the time series in Figure 2, panels (a), (b) and (d).
- Ensemble: 150 replicate runs with seeds 0–149, used for the predation-versus-rabbit scatter in panel (c), which is the model's analogue of the empirical interaction plot.
- Diagnostics: the correlation between lynx predation in year t−1 and the change in kite pairs in year t, restricted to post-crash years, and the correlation between kite pairs and the owl index over the same period.
- Implementation: Python 3 with NumPy and Matplotlib; all parameters sit in a single dictionary at the top of lynx_kite_igp.py.

8 Results of the reference simulation

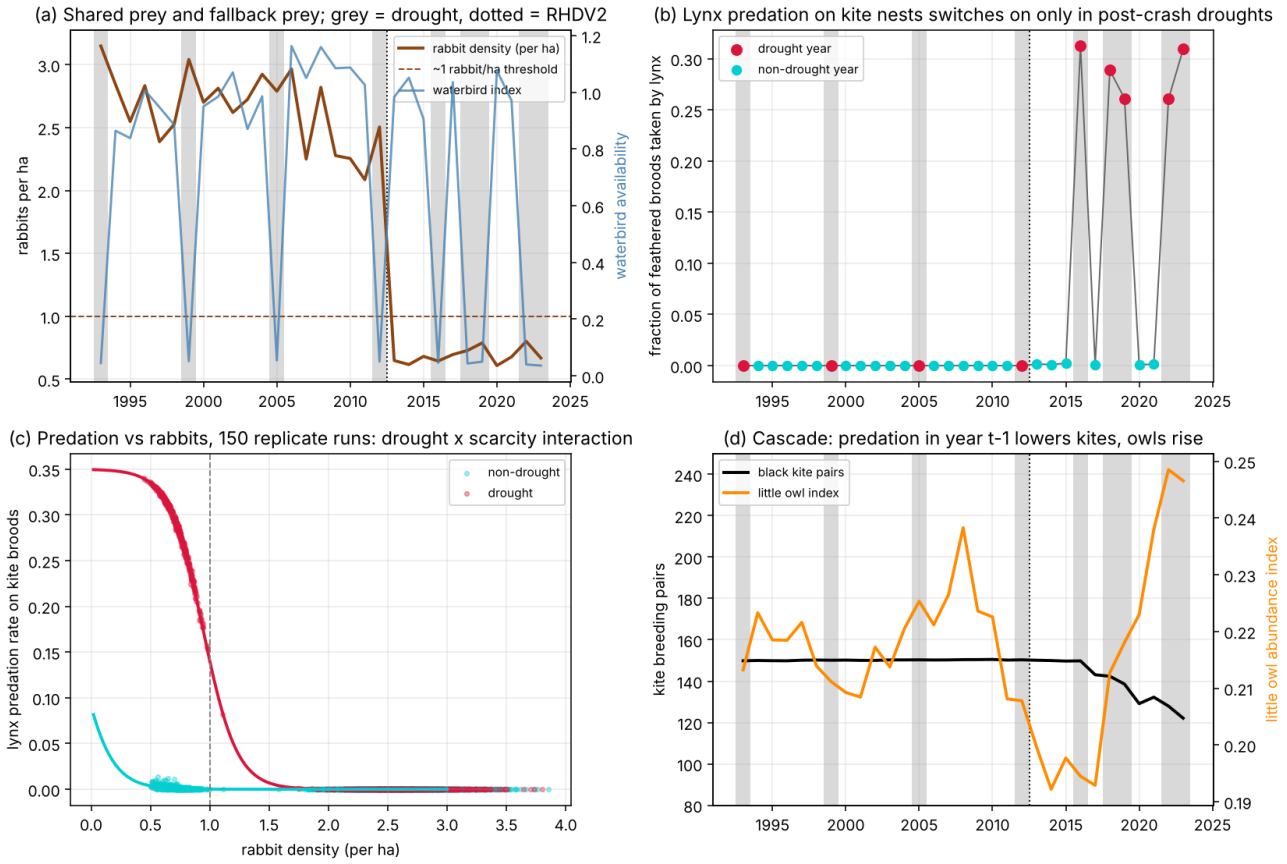


Figure 2. Reference simulation. (a) Rabbit density and waterbird availability; grey bands are drought years and the dotted line is RHDV2 arrival. (b) Fraction of feathered kite broods taken by lynx, with drought years in red and non-drought years in turquoise. (c) Predation rate against rabbit density across 150 replicate runs, with the deterministic switch curves for drought (red) and wet (turquoise) conditions. (d) Kite breeding pairs and the little owl index.

The reference run reproduces the four empirical patterns, as shown in Figure 2:

- Predation is zero in all 20 pre-crash years, including the four pre-crash droughts, because rabbit density of 2.3–3.0 per ha keeps lynx intake above the threshold with or without waterbirds.
- After the crash, mean rabbit density falls from 2.65 to 0.69 per ha. Predation switches on in exactly the five post-crash drought years (2016, 2018, 2019, 2022, 2023) at 26–31% of feathered broods, and stays below 0.3% in the six interleaved wet years.
- Across the ensemble, predation rises steeply with declining rabbit density below about 1 per ha in drought years and is flat near zero at the same rabbit densities in non-drought years, reproducing the empirical interaction.
- Kite pairs decline from the pre-crash steady state of 150 to 122 by 2023, with the decline concentrated in the years following each predation bout; the correlation between predation in year t−1 and the change in kite pairs in year t is −0.81. The owl index rises as kites fall, with a correlation of −0.93 between kite pairs and owls over the post-crash period.

9 Confrontation with the published Source Data

9.1 Data

The Source Data workbook accompanying the article contains, for 25 breeding seasons between 1993 and 2023 with at least 20 assessable nests, the drought indicator, the number of nests predated by lynx, the number of nests assessed at the feathered stage, rabbit density (measured from 2005, reconstructed from the proportion of rabbits in the kite diet before that), a rabbit availability index, and duck abundance in February–May. A separate sheet gives, for 21 years without a year column, kite breeding pairs, little owls counted, and the lynx predation rate in the previous year. Further sheets hold the matched comparisons of predated and control nests, the age, longevity and lifetime reproductive success of marked adults whose broods were taken, and territory abandonment; those were not used here.

In the drought years before the rabbit crash (1993, 1999, 2005, 2012) rabbit density was 4.02, 1.34, 1.50 and 4.54 per ha and predation was 0 of 20, 0 of 47, 2 of 74 and 0 of 98 nests. In the drought years after it (2016, 2018, 2019, 2022, 2023) rabbit density was 0.32, 0.29, 0.21, 0.14 and 0.17 per ha and predation was 9 of 66, 25 of 54, 19 of 58, 18 of 62 and 15 of 52 nests. In the post-crash wet years (2013, 2014, 2015, 2017, 2021) rabbit density was 0.75, 1.55, 0.93, 0.38 and 0.39 per ha and predation was 0 of 79, 3 of 73, 2 of 86, 0 of 83 and 1 of 75 nests.

9.2 Fitting approach

Rather than comparing the free-running simulation of section 8, whose rabbit dynamics are invented, the diet-switch component is tested on its own: the observed rabbit density and drought indicator are used as inputs, and the predicted annual predation rate is compared with the observed counts. Because the data show a low background of opportunistic predation (1 to 4 percent) even when the switch should be closed, a background rate is added to equation (7):

$$p_t = p_0 + \frac{p_{\max}}{1 + \exp[k(I_t - \theta)]} \tag{23}$$

Three forms of the intake I_t are compared: rabbits plus a binary fallback that is present in wet years and absent in drought years, $I_t = R_t + e_W\,(1 - D_t)$; rabbits plus the observed duck index, $I_t = R_t + e_W W_t$ with W_t the duck count divided by 50,000; and rabbits only, $I_t = R_t$. These are set against the logistic generalized linear model structure used in the article, with and without the rabbit × drought interaction:

$$\operatorname{logit}(p_t) = a + bR_t + cD_t + eR_tD_t \tag{24}$$

All models are fitted by maximizing the binomial log-likelihood of the observed predated counts y_t out of n_t nests assessed:

$$\ell = \sum_t \left[y_t \ln p_t + (n_t - y_t) \ln(1 - p_t) \right] \tag{25}$$

Models are compared with Akaike's information criterion, AIC = 2m − 2ℓ, where m is the number of fitted parameters (Burnham and Anderson 2002). Optimization used L-BFGS-B with 40 random restarts because the likelihood surface of the switch is flat along ridges once the switch becomes a step. Observed rates are shown with Jeffreys 95% intervals (Brown et al. 2001).

9.3 Results

Table 3. Model comparison on the 25 annual nest counts. m is the number of fitted parameters; ℓ is the maximized binomial log-likelihood, excluding the combinatorial constant.

Model	m	$-\ell$	AIC	ΔAIC	Fitted values
Switch, rabbits + binary drought fallback	5	272.2	554.3	0.0	$p_{\max} = 0.33$, $\theta = 0.32$, $e_W = 2.4$, $p_0 = 0.014$, $k \to \infty$ (*step*)
GLM, rabbit × drought interaction (as in the article)	4	274.8	557.5	3.2	$a = -4.47$, $b = 0.19$, $c = 4.16$, $e = -2.69$
Switch, rabbits only	4	280.7	569.3	15.0	$p_{\max} = 0.29$, $\theta = 0.32$, $p_0 = 0.014$, $k \to \infty$
Switch, rabbits + duck index	5	280.6	571.2	16.9	$e_W \to 0$, collapses to rabbits only
GLM, rabbit + drought, no interaction	3	294.1	594.2	39.9	$a = -3.05$, $b = -0.91$, $c = 2.19$

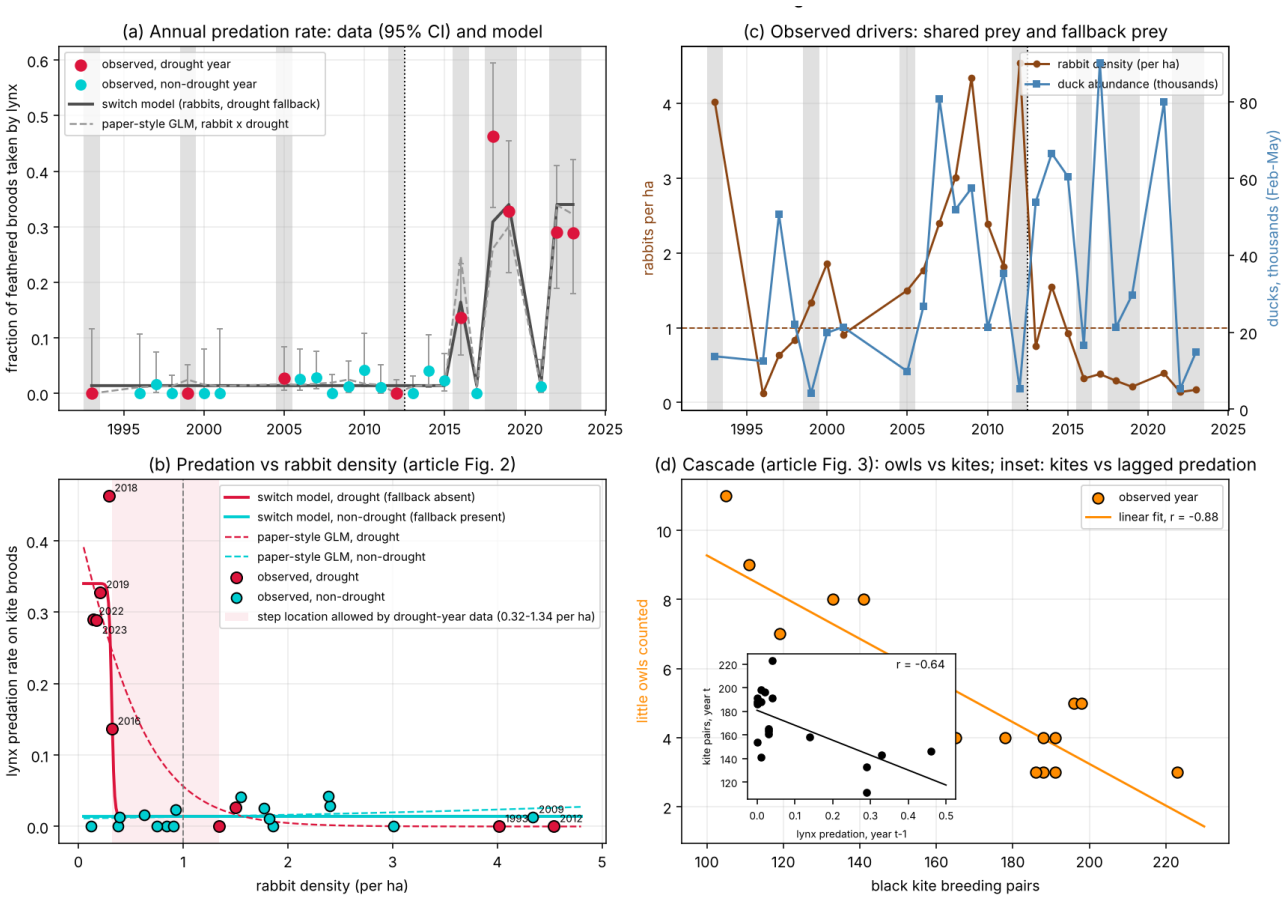


Figure 3. Diet-switch model fitted to the Source Data. (a) Observed annual predation rate (points, Jeffreys 95% intervals; red drought years, turquoise non-drought years) with the fitted switch (solid) and the article-style interaction GLM (dashed). (b) The article's Figure 2 layout: predation against rabbit density, with the fitted switch and GLM curves for drought and non-drought conditions and the range of rabbit densities within which the step must lie. (c) The observed drivers, rabbit density and duck abundance. (d) Little owls against kite pairs (r = −0.88) and, inset, kite pairs against the previous year's lynx predation rate (r = −0.64).

Four results follow (see Figure 3).

- The switch with a binary drought fallback has the lowest AIC. It beats the article's interaction GLM by 3.2 units while using one more parameter, so the two are statistically equivalent descriptions of the data. The switch is not a worse fit for being a mechanistic model.

- The drought term is essential. Removing it from the switch costs 15 AIC units; removing the interaction from the GLM costs 37. This is the article's central finding reproduced with a different model class.
- The fitted switch is a step: the steepness parameter k ran to its upper bound. The step must lie between 0.32 and 1.34 rabbits per ha because no drought year has a rabbit density in that interval; the maximum-likelihood location sits at the lower edge because 2016 (0.32 per ha) had intermediate predation (14 percent). The article's take-off point of about 1 rabbit per ha is where its logistic curve crosses a chosen level, not an observed transition. Any threshold in the bracketed range is consistent with the data.
- The fitted background rate is 1.4 percent of feathered broods per year, and the fitted plateau in drought years is 33 percent. The observed 2018 value (46 percent, 25 of 54) lies above both the switch and the GLM; neither model has a term that would raise 2018 above 2019, 2022 and 2023, which had similar rabbit densities.

In the kite–owl sheet, little owls decline linearly with kite pairs over the 21 years ($r = -0.88$) and kite pairs decline with the previous year's lynx predation rate ($r = -0.64$). The simulation of section 8 produced the same two relationships with correlations of −0.93 and −0.81 (there, measured on the change in kite pairs), so the demographic and cascade components are directionally consistent with the data without having been fitted to them.

9.4 The duck-count test

The Source Data allow a direct test of the waterbird hypothesis adopted in section 4.3. Replacing the binary drought indicator with the observed duck index as the fallback term makes the fit worse by 17 AIC units, and the fitted weight on ducks goes to zero. The reason is visible in the data rather than in the model. In 1996, a wet year, reconstructed rabbit density was 0.12 per ha, the lowest in the series, duck abundance (12,500) was no higher than in several drought years (1993: 13,700; 2016: 16,600; 2023: 15,000), and none of 22 nests was predated. A model in which low rabbits plus low ducks open the switch must predict heavy predation in 1996 and is penalized accordingly; a model in which the switch opens only in drought years classified by flooded area has no such problem. The drought classification therefore carries information that duck counts do not.

Three interpretations are possible. The 1996 rabbit value may be unreliable: it predates the direct censuses and is inferred from the kite diet, and a diet-based estimate can be low because kites were eating something else rather than because rabbits were scarce. Alternatively, the fallback resource removed by drought may not be ducks but other wetland prey that the February–May duck count does not capture. Or the drought effect may not act through lynx diet at all but through access: kite nests in Doñana stand in trees at the edge of the marsh, and a lynx can reach them on foot only when the ground beneath is dry. The model of section 4 is agnostic among these, since W only needs to be present in wet years and absent in drought years, but the mechanism named for W in that section should be regarded as one hypothesis among three until lynx diet or movement data across wet and dry years are available.

10 Limitations and extensions

- In the simulation of section 8 the threshold location and the on/off pattern were calibrated by hand. Section 9 replaces that calibration with a maximum-likelihood fit to the published nest counts, which shows that the switch is at least as consistent with the data as the paper's own statistical model. It does not show that the switch is the only mechanism that would fit, and the demographic and cascade components remain unfitted.
- The model cannot separate nutritional predation from competitor removal, because both predict the same switch. The empirical study leaves the same question open. A version in which the benefit term includes the future reduction in competition for rabbits would be the natural test, but it requires assumptions about lynx cognition that the data do not constrain.
- Lynx numbers are fixed. Adding a lynx numerical response recovers the full Holt–Polis dynamics and would let the model address whether the rabbit crash could eventually suppress lynx enough to switch predation off again.
- The ”rabbit remains under nests” encounter mechanism reported empirically is not represented. A spatially explicit individual-based model, with 4–6 lynx territories, 100–220 kite nests and an encounter rate proportional to the rate at which kites deliver rabbit remains to nests, would make that mechanism explicit and could be fitted to the per-nest data.

- Rabbit disease is imposed as a step change in carrying capacity. Coupling an SIR-type epidemic model for RHDV2 would allow the crash and any partial recovery to emerge from transmission dynamics.
- The identity of the fallback resource removed by drought is unresolved. Duck counts, the obvious candidate, do not improve on the drought indicator in the Source Data (section 9.4), and the one year that most strongly contradicts a duck mechanism (1996) relies on a diet-based rabbit reconstruction. A direct test would need lynx diet data across wet and drought years, or telemetry showing whether lynx reach kite nest trees only when the surrounding marsh is dry.
- The owl cascade is a weak test, since any reduction in kite numbers would produce it. Distinguishing a kite-mediated effect from direct drought effects on owls would require an owl model with its own climate sensitivity.

11 Discussion and conclusion

The question that motivated this study was whether a mathematical or simulation model could replicate the findings of Sergio et al. (2026) in the "spirit" of Lotka–Volterra. The answer is that the findings sit inside the Lotka–Volterra lineage, through intraguild predation theory, but that the classical fixed-coefficient models in that lineage cannot reproduce them, and that one addition is enough to do so: a state-dependent diet switch in the top predator, derived from optimal diet theory. With that addition, a simple annual model reproduces the twenty years of negligible predation, the abrupt onset in post-crash drought years, the flat response in wet years at the same rabbit densities, the one-year lag between predation and kite abundance, and the inverse relationship between kites and little owls. Fitted to the published nest counts, the switch is statistically equivalent to the interaction GLM used in the article (ΔAIC = 3.2 with one more parameter) and, like the GLM, loses between 15 and 40 AIC units if the drought term is removed. The article's central claim, that disease and drought act jointly and neither is sufficient alone, is therefore recovered by an independent model class built from a foraging rule rather than from a regression.

Two points go beyond the article. First, the data locate the rabbit-density step only to the interval between 0.32 and 1.34 per ha, because no drought year falls inside it. The stated take-off near 1 per ha is a property of the fitted logistic curve rather than an observed transition, and any threshold in that interval is equally consistent with the counts. Second, the published duck counts do not account for the drought effect: a switch that uses them as the fallback term collapses to rabbits only, largely because 1996 combined very low reconstructed rabbit density, drought-level duck numbers and zero predation. Whatever drought removes from the lynx's options, it is not captured by February–May duck abundance. The candidates are other wetland prey, an unreliable 1996 rabbit estimate, or physical access to nest trees once the marsh beneath them is dry. These are distinguishable with lynx diet data or telemetry across wet and drought years, and the model is agnostic among them.

The model makes two predictions that the data do not yet test. Because the switch depends on the conjunction of drought and rabbit scarcity, predation on kites is expected in every future drought year while rabbit density stays below the step, and in none of the wet years. The demographic component then implies a kite decline whose rate scales with drought frequency, and an owl increase that tracks it. Conversely, a recovery of rabbits above the step, whether through disease resistance, management or habitat change, is predicted to switch predation off in drought years as well, which is the lever the model offers to management. Both statements rest on holding lynx numbers constant and on a fallback whose identity is unresolved, and both would be sharpened by replacing the aggregate switch with the individual-based, spatially explicit version outlined in section 10.

A model can replicate the article's findings, and the relevant mathematics is Lotka–Volterra by descent, but the ingredient that matters is behavioral rather than demographic. The results are explained not by how many lynx or kites there are but by a decision rule that a single lynx applies when its preferred prey and its fallback disappear together.

References

Abrams, P. A. & Matsuda, H. (1996). Positive indirect effects between prey species that share predators. Ecology 77, 610–616.

Beverton, R. J. H. & Holt, S. J. (1957). On the Dynamics of Exploited Fish Populations. Fishery Investigations Series II, Vol. 19. Ministry of Agriculture, Fisheries and Food, London.

Caswell, H. (2001). Matrix Population Models: Construction, Analysis, and Interpretation, 2nd edn. Sinauer, Sunderland, MA.

Brown, L. D., Cai, T. T. & DasGupta, A. (2001). Interval estimation for a binomial proportion. Statistical Science 16, 101–133.

Burnham, K. P. & Anderson, D. R. (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edn. Springer, New York.

Charnov, E. L. (1976). Optimal foraging: attack strategy of a mantid. American Naturalist 110, 141–151.

Dalton, K. P., Nicieza, I., Balseiro, A., Muguerza, M. A., Rosell, J. M., Casais, R., Álvarez, Á. L. & Parra, F. (2012). Variant rabbit hemorrhagic disease virus in young rabbits, Spain. Emerging Infectious Diseases 18, 2009–2012.

Delibes-Mateos, M., Redpath, S. M., Angulo, E., Ferreras, P. & Villafuerte, R. (2007). Rabbits as a keystone species in southern Europe. Biological Conservation 137, 149–156.

Hin, V., Schellekens, T., Persson, L. & de Roos, A. M. (2011). Coexistence of predator and prey in intraguild predation systems with ontogenetic niche shifts. American Naturalist 178, 701–714.

Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12, 197–229.

Holt, R. D. & Polis, G. A. (1997). A theoretical framework for intraguild predation. American Naturalist 149, 745–764.

Křivan, V. (2000). Optimal intraguild foraging and population stability. Theoretical Population Biology 58, 79–94.

Křivan, V. & Diehl, S. (2005). Adaptive omnivory and species coexistence in tri-trophic food webs. Theoretical Population Biology 67, 85–99.

Lotka, A. J. (1925). Elements of Physical Biology. Williams & Wilkins, Baltimore.

Lourenço, R., Penteriani, V., Rabaça, J. E. & Korpimäki, E. (2014). Lethal interactions among vertebrate top predators: a review of concepts, assumptions and terminology. Biological Reviews 89, 270–283.

Monterroso, P., Garrote, G., Serronha, A., Santos, E., Delibes-Mateos, M., Abrantes, J., Pérez de Ayala, R., Silva, F., Castro, F., Esteves, P. J., Villafuerte, R. & Alves, P. C. (2016). Disease-mediated bottom-up regulation: an emergent virus affects a keystone prey, and alters the dynamics of trophic webs. Scientific Reports 6, 36072.

Mylius, S. D., Klumpers, K., de Roos, A. M. & Persson, L. (2001). Impact of intraguild predation and stage structure on simple communities along a productivity gradient. American Naturalist 158, 259–276.

Palomares, F. & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. American Naturalist 153, 492–508.

Palomares, F., Delibes, M., Revilla, E., Calzada, J. & Fedriani, J. M. (2001). Spatial ecology of Iberian lynx and abundance of European rabbits in southwestern Spain. Wildlife Monographs 148, 1–36.

Polis, G. A., Myers, C. A. & Holt, R. D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics 20, 297–330.

Ricker, W. E. (1954). Stock and recruitment. Journal of the Fisheries Research Board of Canada 11, 559–623.

Ritchie, E. G. & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12, 982–998.

Sergio, F. & Hiraldo, F. (2008). Intraguild predation in raptor assemblages: a review. Ibis 150 (Suppl. 1), 132–145.

Sergio, F., Blas, J., Forero, M. G., Fernández, N., Donázar, J. A. & Hiraldo, F. (2005). Preservation of wide-ranging top predators by site-protection: black and red kites in Doñana National Park. Biological Conservation 125, 11–21.

Sergio, F., Natsukawa, H., Tanferna, A., Chicano, J., Carro, F., Soriguer, R. C., Hiraldo, F. & Blas, J. (2026). Drought and disease trigger novel interactions among top predators. Nature. doi:10.1038/s41586-026-11194-z

Stephens, D. W. & Krebs, J. R. (1986). Foraging Theory. Princeton University Press, Princeton, NJ.

Stephens, D. W., Brown, J. S. & Ydenberg, R. C. (eds) (2007). Foraging: Behavior and Ecology. University of Chicago Press, Chicago.

Volterra, V. (1926). Fluctuations in the abundance of a species considered mathematically. Nature 118, 558–560.