Behavioural strategy and predator control: a coupled evolutionary predator-prey model for kiwi conservation in New Zealand

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Keywords: Evolutionary game theory, Lotka-Volterra model, replicator dynamics, predator-prey dynamics, foraging strategy, predator control, kiwi conservation, behavioural ecology, New Zealand conservation

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Abstract

Conservation management of endangered species can be enhanced by quantitative frameworks that simultaneously model behavioural adaptations alongside population dynamics. This paper presents a Coupled Evolutionary Predator-Prey Model (CEPPM) that integrates replicator dynamics from Evolutionary Game Theory with an extended Lotka-Volterra predator-prey framework, applied to kiwi (*Apteryx spp.*) under stoat (*Mustela erminea*) predation in New Zealand, with parameters grounded in published field data.

We identify three analytically derived stoat-removal thresholds (h) that partition management outcomes into four qualitatively distinct regimes: below an effective kiwi recovery threshold $h_{survival} \approx 0.165$, kiwi cannot begin recovery regardless of intervention timing; between $h_{survival}$ and an analytical stoat suppression threshold $h_{crit} = 0.25$, kiwi recover while stoats persist at a low demographic floor; between h_{crit} and a true stoat eradication threshold $h_{erad} \approx 0.33$, a "kiwi bonus zone" allows stoats to persist (counterintuitively, even as suppression intensifies) because the recovering kiwi population itself subsidises the remaining stoats as prey; and above h_{erad}, stoats are driven to zero regardless of kiwi abundance. Threshold locations are robust to parameter variation: across literature-derived ranges, h_{crit} varies 0.14–0.44, h_{erad} 0.21–0.51, and $h_{survival}$ 0.07–0.33, with uncertainty driven primarily by stoat demography.

The CEPPM incorporates lowering the risk of open foraging through predator suppression, thereby accelerating kiwi recovery. Open foraging proportions at equilibrium range from ≈44% under unmanaged predation to ≈76% under full stoat suppression, with an analytically derived survival-enabling proportion of ≈41%. This behavioural trajectory is a measurable conservation outcome in its own right, and its omission from population-only models risks over- or under-estimating recovery speed. Interlinking behavioural strategy evolution with population dynamics reveals a non-linear threshold structure and a behavioural dimension of recovery unavailable from either framework alone. Models of this kind can help conservation analyses better represent ecological processes and inform more precisely targeted policy decisions.

Introduction

The management of endangered species requires frameworks that capture both population dynamics and the behavioural adaptations of individuals over time. Traditional conservation modelling has relied primarily on demographic frameworks such as Lotka-Volterra predator-prey systems (Lotka 1925; Volterra 1926), which treat populations as behaviourally uniform. Evolutionary game theory (EGT) and replicator dynamics offer a complementary perspective, describing how the frequency of competing strategies evolves as a function of relative fitness (Maynard Smith & Price 1973; Taylor & Jonker 1978; Börgers & Sarin 1997). Despite substantial theoretical work coupling EGT with predator-prey dynamics (Křivan 2007; Kooi 2015; Araújo 2025), applications to the conservation management of specific endangered species remain rare.

New Zealand's native fauna, isolated from mammalian predators for 85 million years, is acutely vulnerable to introduced predators (King & Powell 2007). The stoat (Mustela erminea) is the primary driver of kiwi (Apteryx spp.) decline on the mainland (McLennan et al. 1996), with the current population of ~68,000 birds declining at ~2% per year absent management. This trajectory would produce a 60% decline within three generations (Robertson et al. 2011; Department of Conservation 2018). Predator control, principally via aerial 1080 application across ~1.8 million hectares of conservation land, and captive-rear-and-release programmes (Operation Nest Egg), has demonstrated substantial improvements in chick survival and population growth (Germano et al. 2015; Colbourne et al. 2005; Department of Conservation 2024). Nationally, the Predator Free 2050 initiative and DOC's Kiwi Recovery Plan target 100,000 birds by 2030 (Department of Conservation 2018), though it remains unclear whether existing control strategies are sufficient at the required scale.

The kiwi-stoat system is well suited to coupled foraging behaviour-demographic modelling. Open foraging offers higher food intake at greater predation risk, while cover foraging trades food for safety, producing a frequency- and density-dependent payoff structure; and stoats are dietary generalists (kiwi <5% of diet; Murphy & Dowding 1995), giving their population dynamics a complexity beyond a simple predator-prey pairing. Strategy dynamics here represent intra-generational learned adaptation, not genetic selection, consistent with the use of the Replicator Dynamic form to model such behaviour (Cross 1973; Slagsvold & Wiebe 2011; Aplin et al. 2015). Decades of New Zealand field monitoring provide sufficient data to parameterise such a model (Alterio et al. 1999; Murphy & Dowding 1994; Barlow & Barron 2005).

Existing studies have modelled kiwi population dynamics without incorporating foraging behaviour (Basse et al. 1999; Barlow & Barron 2005), despite evidence that foraging strategy materially affects population outcomes generally (Lima & Dill 1990) and in kiwi specifically (Cunningham & Castro 2011). Where behaviour and demography have been linked, this has used instantaneous individual-level optimisation (Cressman et al. 2004; Křivan & Cressman 2009) or purely theoretical treatments (Auger et al. 2002; Kooi 2015; Karmakar et al. 2025) rather than population-level replicator dynamics applied to a specific, field-parameterised ecosystem. This gap motivates the Coupled Evolutionary Predator-Prey Model (CEPPM) developed here, which integrates dynamic, stoat-density-dependent payoffs into the replicator equation, and foraging proportion into the L-V equations to determine whether coupled behavioural-demographic modelling can predict kiwi-stoat

conservation outcomes, identify the harvest thresholds for distinct management regimes, and derive the associated foraging behaviour.

Model Development

Methodology. The CEPPM was developed in three stages: (i) an evolutionary game theory (EGT) model with replicator dynamics established equilibrium foraging strategies; (ii) the Lotka-Volterra (L-V) equations were extended to include logistic kiwi growth, a Holling Type II predation ceiling, and generalised (non-kiwi-dependent) stoat dynamics; and (iii) the two frameworks were bi-directionally coupled via stoat-density-dependent payoffs and strategy-dependent population parameters. Parameters were sourced from published New Zealand field data wherever possible, with derivations documented where direct estimates were unavailable. The model was implemented in Python, run across seven predator-control scenarios varying harvest rate and intervention timing, subjected to sensitivity analysis, and compared against analytically derived minimum kiwi-survival conditions and observed kiwi monitoring outcomes. Software development and debugging for the CEPPM implementation were assisted by Claude (Anthropic); full details of AI tool use are provided under Acknowledgments.

The model tracks three coupled states simultaneously: open foraging proportion $x(t)$, kiwi population $K(t)$, and and stoat population $S(t)$, as shown in Figure 1 and Equations 1-3.

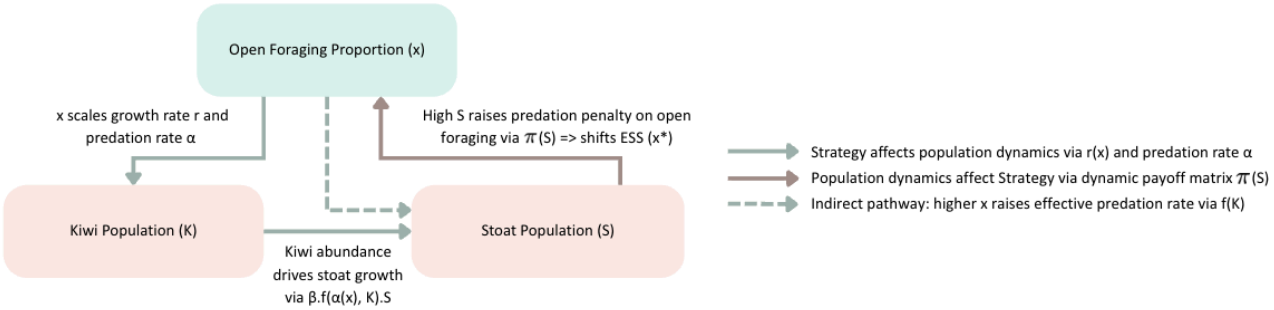

Figure 1. *Three-way feedback loop between kiwi foraging behaviour and species populations as modeled by CEPPM*

CEPPM Foraging Strategy: $$\frac{dx}{dt} = \kappa_{learn} \cdot x \cdot (\hat{\pi}_A(x, S) - \bar{\hat{\pi}}(x, S)) \quad (1)$$

CEPPM Kiwi Population: $$\frac{dK}{dt} = r(x) \cdot K \cdot (1 - \frac{K}{K_{max}}) - f(\alpha(x), K) \cdot S \quad (2)$$

CEPPM Stoat Population: $$\frac{dS}{dt} = r_{stoat} \cdot S(1 - \frac{S}{S_{max}}) + \beta \cdot f(\alpha(x), K) \cdot S - \delta S - hS \quad (3)$$

Where x = open foraging frequency; κ_{learn} = per-capita behavioural adaptation rate; π = strategy payoff; S = stoat population per 1,000 ha; K = kiwi population per 1,000 ha; r = kiwi intrinsic growth rate; K_{max} = kiwi habitat carrying capacity per 1,000 ha; α= stoat predation rate; r_{stoat} = stoat intrinsic growth rate from non-kiwi prey; S_{max} = theoretical ceiling of stoat growth from non-kiwi prey; β = stoat conversion efficiency; δ = stoat death rate; h = annual harvest rate

Stage 1. *EGT Model Static Payoff Matrix & Replicator Dynamics*

A 2×2 payoff matrix (Table 1) represents net foraging utilities (nutritional reward and habitat comfort less crowding costs) for kiwi in the absence of predation pressure, tracking the proportion x of kiwi using open (Strategy A) versus cover (Strategy B) foraging.

Table 1*. Payoff values for Open and Cover foraging strategies*

		Others' Strategy	
		A (open)	B (cover)
K_i Strategy	A (open)	a	b
K_i Strategy	B (cover)	c	d

Payoff functions and the replicator dynamic equation *f(x)* are given below, where κ_{learn} is the per-capita behavioural adaptation rate governing how quickly strategy proportions respond to payoff differences:

$$\pi_A(x) = x \cdot a + (1 - x) \cdot b \,;\, \pi_B(x) = x \cdot c + (1 - x) \cdot d$$

$$\bar{\pi}(x) = x \cdot \pi_A(x) + (1 - x) \cdot \pi_B(x) \tag{4}$$

$$f'(x) = \frac{d}{dx}\left(\frac{dx}{dt}\right) = \frac{d}{dx}\left(\kappa_{learn} \cdot x \cdot (\pi_A(x) - \bar{\pi}(x))\right) \tag{5}$$

The ESS x^* is the interior fixed point at which expected payoffs of A and B are equal, and is stable where $f'(x^*) < 0$.

Stage 2. *Extended Lotka-Volterra (L-V) Model*

The classic L-V model allows unbounded kiwi growth, an unbounded predation term αKS, and total stoat dependence on kiwi prey. These are resolved via logistic kiwi growth limited by K_{max}, a saturating Holling Type II predation response $f(K)$ that avoids the atto-fox problem (Fowler 2021), and a generalised stoat equation split into non-kiwi intrinsic growth, a kiwi predation bonus, natural mortality, and a continuous proportional annual harvest term h, consistent with year-round trapping in New Zealand sanctuaries (Department of Conservation 2024).

$$f(K) = \frac{\alpha K}{1 + \alpha H K} \quad \textit{where H = Holling Type II handling time}$$

$$\frac{dK}{dt} = r \cdot K \cdot \left(1 - \frac{K}{K_{max}}\right) - f(K) \cdot S \tag{6}$$

$$\frac{dS}{dt} = \underbrace{r_{stoat} \cdot S \cdot \left(1 - \frac{S}{S_{max}}\right)}_{\text{Non-kiwi logistic growth}} + \underbrace{\beta \cdot f(K) \cdot S}_{\text{Kiwi bonus}} - \underbrace{\delta S}_{\text{Natural mortality}} - \underbrace{hS}_{\text{Harvest}} \tag{7}$$

The generalised stoat equation permits persistence on non-kiwi prey independent of kiwi abundance. We define S_{floor} as the stoat density at which non-kiwi logistic growth exactly balances natural mortality, representing the biological lower bound on unmanaged stoat density. Below S_{floor} the natural non-kiwi logistic growth less natural mortality is clamped at zero rather than allowed to go negative, reflecting abundant availability of non-kiwi prey. Harvest mortality bypasses the floor entirely, allowing sufficiently high h to drive stoats toward eradication:

$$r_{stoat} \cdot (1 - \frac{S_{floor}}{S_{max}}) = \delta \Rightarrow S_{floor} = S_{max} \cdot (1 - \frac{\delta}{r_{stoat}})$$

$$g(S) = r_{stoat} \cdot S \cdot (1 - \frac{S}{S_{max}}) - \delta S$$

For any $h > 0$, stoats find a harvest-modified equilibrium as shown below:

$$S^*(h) = S_{max} \cdot (1 - (\delta + h)/r_{stoat}) < S_{floor} \quad (8)$$

This structure defines the harvest regimes summarised in Table 5, where h_{crit} is the rate at which the non-kiwi equilibrium collapses to zero and h_{erad} is the true eradication threshold accounting for the kiwi predation bonus.

Stage 3. *Coupled Evolutionary Predator-Prey Model (CEPPM)*

The model couples x, K, and S bi-directionally: (i) kiwi growth rate r and predation rate α depend on x; (ii) kiwi population K drives stoat density via the predation-bonus term β·f(α(x),K)·S; and (iii) stoat density S feeds back onto foraging payoffs via a sigmoid penalty, closing the loop through the replicator equation. Payoffs are adjusted via a sigmoid penalty p·σ(S), where k is the sigmoid steepness, S_{mid} the inflection point, and p_{open}/p_{cover} the maximum penalties for open/cover foraging. Above S_{mid}, cover foraging dominates; below it, open foraging is rewarded as predation pressure falls. A lower bound of 0.01 is applied on all adjusted payoffs to preserve biological plausibility.

$$\sigma(S) = \frac{1}{1+e^{-k(S-S_{mid})}}$$

$$\hat{\pi}_{ij}(S) = max(\pi_{ij} - p_i \cdot \sigma(S),\ 0.01)$$

where (i,j) denotes a cell in the payoff matrix and $p_i = p_{open}$ for row A (open foraging) and $p_i = p_{cover}$ for row B (cover foraging), applied uniformly across both columns (j)

$$\frac{dx}{dt} = \kappa_{learn} \cdot x \cdot (\hat{\pi}_A(x,S) - \bar{\hat{\pi}}(x,S)) \quad \rightarrow(1)$$

Kiwi population, $K(t)$, is modeled by the *Kiwi Equation* by modifying Eq. 6 such that the effective growth rate r and predation rate α depend on the open foraging strategy proportion x.

$$r(x) = r_{base} \cdot \frac{\bar{\pi}(x)}{\bar{\pi}(x^*)}$$

Where r_{base} is the L-V model kiwi intrinsic growth rate r, and $\bar{\pi}(x)$ and $\bar{\pi}(x^*)$ are the average payoffs from the EGT model for a given strategy proportion x and EGT equilibrium x^*

$$\alpha(x) = \alpha_{base} \cdot [v_{open} \cdot x + v_{cover} \cdot (1 - x)]$$

Where v_{open} and v_{cover} are the vulnerability weights for open vs. cover foraging respectively

$$\frac{dK}{dt} = r(x) \cdot K \cdot (1 - \frac{K}{K_{max}}) - f(\alpha(x), K) \cdot S \quad \rightarrow(2)$$

Stoat population, $S(t)$, is modeled by the *Stoat Equation*, which takes the same form as Eq. 7, except that the predation term is now strategy-dependent.

$$\frac{dS}{dt} = r_{stoat} \cdot S(1 - \frac{S}{S_{max}}) + \beta \cdot f(\alpha(x), K) \cdot S - \delta S - hS \quad \rightarrow(3)$$

An intervention time t* switches the system from natural to managed dynamics (harvest rate h active for t ≥ t*). This fully specifies the model via the equations introduced above (Eqs. 1-3).

Kiwi growth requires $dK/dt \approx K \cdot (r(x) - \alpha(x) \cdot S) > 0$. Substituting the strategy-dependent parameters yields the maximum viable stoat density and minimum survival harvest rate with the corresponding survival-enabling foraging proportion x_{survival} obtained by solving $R'(x) = 0$ and testing for maxima:

$$S < \frac{r_{base}}{\alpha_{base} \cdot \bar{\pi}(x^*)} \cdot \frac{\bar{\pi}(x)}{[v_{open} \cdot x + v_{cover} \cdot (1-x)]} \equiv C \cdot R(x)$$

$$S_{critical} = C \cdot \max_{x \in [0,1]} R(x) \quad (10)$$

$$h_{survival} = r_{stoat} \cdot (1 - \frac{S_{critical}}{S_{max}}) - \delta \quad (11)$$

This bi-directional coupling means predator control reduces S, which rewards open foraging, raises $r(x)$, and accelerates kiwi recovery. The post-intervention behavioural shift is a prediction unique to the CEPPM and is examined quantitatively in Results.

Parametric Data

Parameters were sourced from published New Zealand field data wherever possible, prioritising primary studies over modelled estimates (Table 2). EGT payoff values reflect net food reward, crowding cost, and cover-foraging habitat comfort reflecting predation-independent shelter value (Taborsky & Taborsky 1995; Jamieson et al. 2016), calibrated to produce a plausible interior ESS with sensitivity analysis as the primary quantitative defence. L-V parameters are derived from DOC monitoring and stoat demographic literature (King 1983; Powell & King 1997; Murphy & Dowding 1994, 1995; Barlow & Barron 2005). Sigmoid penalty parameters, for which no published

stoat-density/foraging-shift data exist, were calibrated so the behavioural transition completes before stoat densities associated with unsustainable chick survival occur (McLennan et al. 1996).

Table 2. *Model Component Parameters*

Symbol	Value	Description	Basis for Assumption
a	0.35	Payoff to open forager meeting open forager	Moderate reward reflecting intra-specific competition for exposed foraging sites
b	0.55	Payoff to open forager meeting a cover forager	Highest individual reward as open forager gains full food benefit when competitors forage elsewhere
c	0.45	Payoff to cover forager meeting an open forager	High reward as cover forager benefits from habitat comfort while open foragers do not
d	0.20	Payoff to cover forager meeting cover forager	Lowest utility due to lower food reward and higher crowding costs
x_0	0.30	Initial open foraging proportion	Conservative, reflecting high unmanaged predation pressure
κ_{learn}	1.5 /year	Behavioural adaptation or 'learning' rate	Illustrative; anchored to habitat-use flexibility (Dixon 2015; Massaro et al. 2008). Robustness tested via sensitivity analysis.
r	0.05 /yr	Kiwi intrinsic per capita growth rate	Conservative managed-population estimate (DOC 2018 Kiwi Recovery Plan)
α	0.044	Per capita predation rate constant	dK/dt = -0.02 (the unmanaged observed decline), so α.S*=r+0.02; at S*≅1.6 stoats/1000 ha, α=0.044; consistent with McLennan et al. (1996) predation outcome data
β	0.0175	Stoat conversion efficiency from kiwi predation	Using an observed kiwi density of 20 birds/sq km gives β = δ/B* = 0.0175; kiwi <5% of stoat diet (Murphy & Dowding 1995)
H	0.1	Holling Type II handling time	Mustelid parameterisation (Holling 1959); sets ceiling of 10 kiwi/stoat/yr
K_0, K_{max}	20, 150	Initial kiwi density; Carrying capacity	DOC 2018; territory size 5–50 ha/pair (Robertson 2013)
S_0, S_{max}	5, 8	Initial stoat density; Non-kiwi carrying capacity	Home-range estimates (Murphy & Dowding 1994; King & Powell 2007)
r_{stoat}, δ	0.60/yr, 0.35/yr	Stoat intrinsic growth rate (non-kiwi prey); Death rate	Barlow & Barron 2005 (non-mast forest); Powell & King 1997
k, S_{mid}	3.0, 1.0	Sigmoid steepness, Inflection point	Calibrated: transition largely complete before S≈1.5, where chick survival collapses (McLennan et al. 1996)
p_{open}, p_{cover}	0.30, 0.15	Maximum penalties on open and cover foraging payoffs	Calibrated so adjusted ESS <0.5 at S≈1.5
v_{open}, v_{cover}	1.30, 0.70	Vulnerability weights	Assumed ~1.86:1 ratio; no direct kiwi-specific data
π_{floor}	0.01	Minimum payoff floor	Ensures non-negativity; no empirical basis, doesn't affect outcomes materially

Table 3. *Derived Parameters*

Symbol	Value	Description	Basis for Derivation
S_{floor}	3.333	$S_{max}\cdot(1-\delta/r_{stoat})$	Non-kiwi stoat equilibrium at h=0. Stoat density sustained by rodents/invertebrates alone in absence of harvest
S*(h)	varies	$S_{max}\cdot(1-(\delta+h)/r_{stoat})$	Harvest-modified stoat equilibrium at rate h; declines linearly until $h=h_{crit}$
h_{crit}	0.25	$r_{stoat}-\delta$	Harvest rate at which S*(h) collapses to zero. Non-kiwi prey alone cannot sustain positive stoat population above this rate
$h_{survival}$	0.165	$r_{stoat}\cdot(1-S_{critical}/S_{max})-\delta$	Effective kiwi recovery threshold below which kiwi extinction proceeds regardless of intervention timing
h_{erad}	0.3258	$h_{crit}+\beta\cdot f(K_{max})$	Minimum harvest rate at which stoats are driven towards zero, calculated using CEPPM parameter values

Results and Discussion

Standalone EGT. Using the parameter values for payoffs and behavioural adaptation rate, the replicator dynamic equation (5) yields an equilibrium x*= 0.7778 and f'(x*)= -0.7778 (< 0). This is a stable, self-correcting equilibrium of ~78% open foraging in the absence of predation pressure.

Scenario Analysis. Simulation across seven predator-control scenarios that varied harvest rate h and intervention year t over a fixed simulation horizon of T_{max}=200 years (Table 4, Figure 2) reveals a strongly non-linear relationship between harvest intensity and kiwi recovery, with regime shifts at the three thresholds identified analytically (Table 5). Below $h_{survival}\approx0.165$, kiwi decline to extinction regardless of stoat suppression achieved (Scenarios Control, 1). A 10-point harvest increase from h=0.10 to h=0.20 produces an existential difference (extinction vs. survival), while a further 20-point increase from h=0.40 to h=0.60 (even at a shorter intervention time) produces only a negligible long-run difference (K=149.7 vs 149.9 at t=200), illustrating that management effort is best allocated relative to regime boundaries rather than treated as a uniform trade-off. Between h_{crit}=0.25 and $h_{erad}\approx0.33$, stoats persist solely through the kiwi predation bonus while kiwi recover substantially (K=85.6–143.7; Scenarios 2b, 2c). Above h_{erad}, stoats are driven to eradication and kiwi converge to the same long-run outcome (K≈150) regardless of the harvest intensity or intervention timing used to get there (Scenarios 3a–3b). Figure 3 confirms these regime boundaries emerge continuously across the full harvest-rate range, not only at the seven sampled scenarios.

Table 4. *Simulation outputs for seven predator control scenarios*

Scenario	Description	Regime	t=0 x%	t=10 x%	t=25 x%	t=50 x%	t=100 x%	t=200 x%	Kiwi (K) t=200	Stoat (S) t=200
Control	No intervention	Baseline	30.0	41.4	44.2	44.5	44.5	44.5	0.0	3.333
1	yr 20 | h=0.10	Failed Management	30.0	41.4	44.3	45.8	46.0	46.0	0.0	2.000
2a	yr 20 | h=0.20	Partial Recovery	30.0	41.4	44.8	62.9	67.7	65.7	17.1	0.822
2b	yr 20 | h=0.25	h_{crit} - Kiwi Bonus	30.0	41.4	45.5	70.6	74.8	69.6	85.6	0.648
2c	yr 20 | h=0.30	Kiwi bonus zone	30.0	41.4	46.6	73.5	76.1	75.9	143.7	0.060
3a	yr 10 | h=0.40	Full suppression	30.0	41.5	68.4	75.8	76.2	76.2	149.7	0.000
3b	yr 2 | h=0.60	Intensive Management	30.0	59.5	74.2	76.1	76.2	76.2	149.9	0.000

x_0=30% K_0=20 S_0=3 | S_{Floor}=3.333 h_{crit}=0.25 h_{erad}=0.33 | Effective recovery threshold h=0.165 | T=200 years

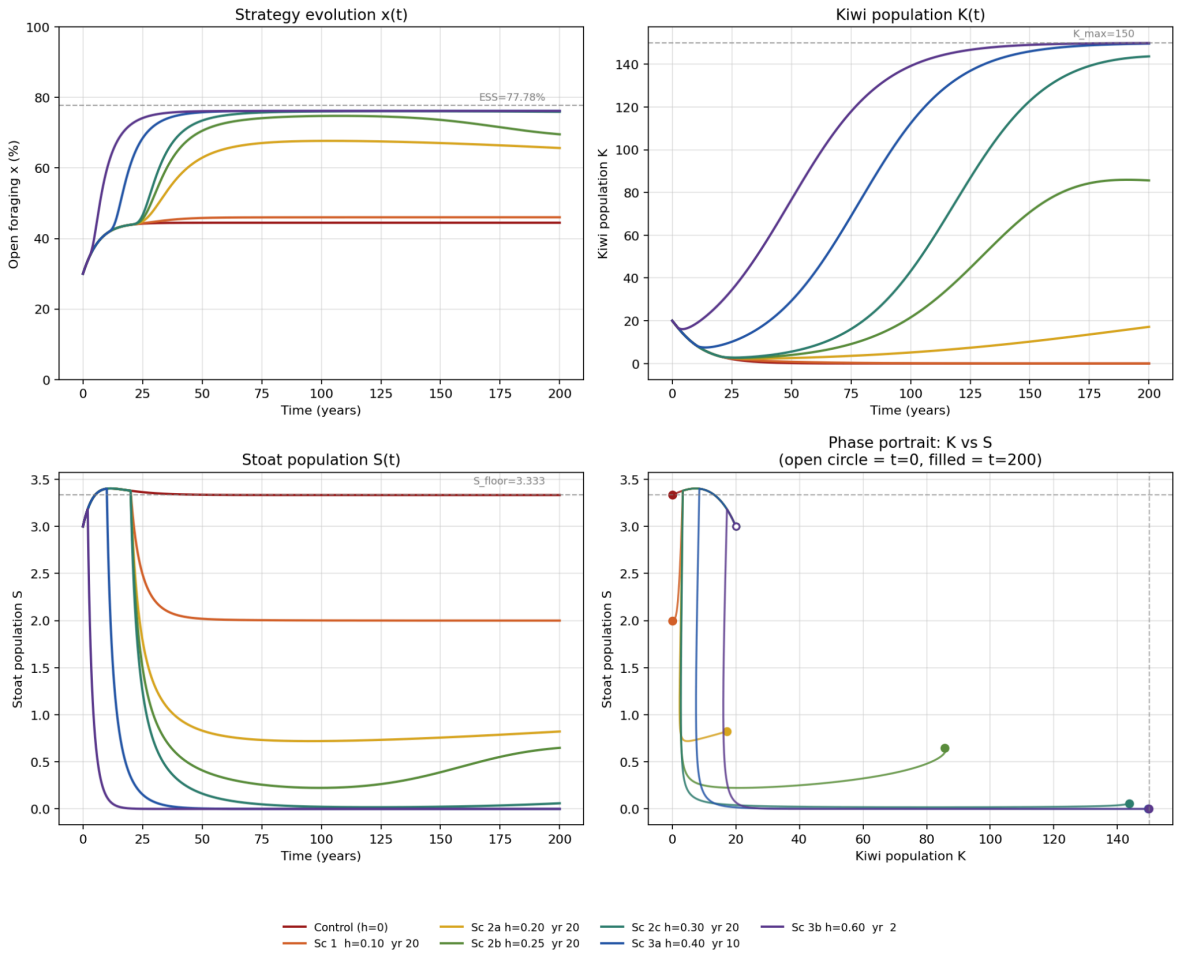

Figure 2. *CEPPM state variable changes over time, compared across the seven scenarios*

Table 5. *Parameterisation of harvest regimes*

Condition	**Harvest regime**	**Population Outcomes at t=200**	**Scenario**
$h = 0$	No management	K=0; no interior coexistence equilibrium; S=3.33 > S_{floor}	Control
$0 < h < 0.25$	Light management	Kiwi may survive at partial recovery below K_{max}; At h=0.10, S=2.0, K=0; At h=0.20, S=0.822, K=17.14	1, 2a
$h = 0.25$	Stoat suppression threshold	Substantial kiwi recovery despite stoat persistence; S=0.649, K=85.64	2a
$0.25 < h < 0.33$	Moderate management	Robust to near full kiwi recovery despite stoat persistence; S=0.060, K=143.67	2b, 2c
$h \geq 0.33$	Active to Intensive management	Full stoat suppression; kiwi recover towards K_{max}; S⟶0, K⟶150; faster trajectory at higher h	3a, 3b

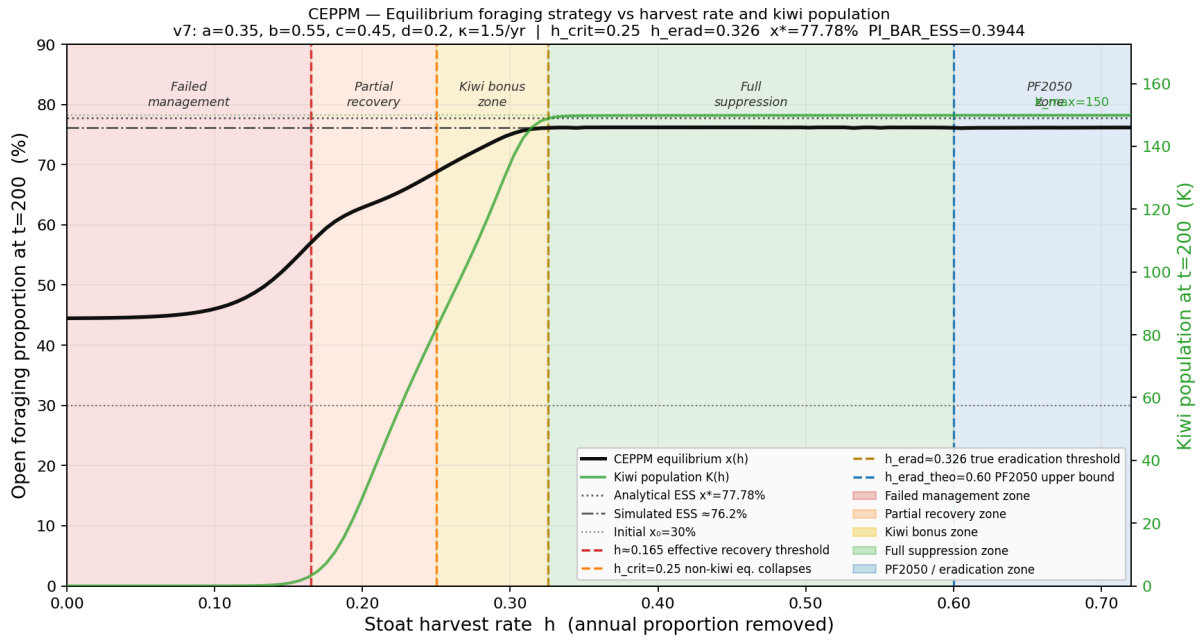

Figure 3. Equilibrium open foraging strategy at t=200 vs. harvest rate and kiwi population (intervention year = 5)

Findings Unique to the CEPPM. Three phenomena emerge from the coupled model that neither standalone component can replicate (Supplement S6). First, the standalone EGT converges to the same analytical ESS (x*=77.78%) regardless of harvest rate, unable to distinguish a managed from an unmanaged population, while the CEPPM instead produces scenario-dependent equilibria ranging from ~44–46% (extinction) to ~76% (full recovery), reflecting the actual predation environment. Second, a survival-enabling strategy boundary is derived analytically (Eqs. 10–11), illustrating that kiwi require ≈40.6% open foraging to sustain positive growth at the maximum viable stoat density ($S_{critical}$≈1.128/1,000 ha), yielding $h_{survival}$≈0.1654, which is consistent with the independent simulation sweep (≈0.163-0.165). Above this threshold, predator control progressively releases the population from the survival constraint, driving open foraging toward the higher dynamic ESS (~76.2%) and accelerating recovery. This mechanism is invisible to standalone demographic models. Third, the CEPPM diverges modestly but systematically from a behaviourally-static L-V model. As open foraging rises toward the ESS, kiwi growth rate r(x) increases but predation exposure α(x) also rises (open foragers carry ~1.3× the vulnerability weight of cover foragers), partially offsetting the growth benefit. The net effect remains positive in that the CEPPM recovers faster than the static L-V predicts but the mechanism involves simultaneous, partially opposing behavioural effects that a behaviourally static model cannot represent.

Sensitivity and Robustness. Bifurcation analysis confirms that all three harvest thresholds correspond to exact transcritical bifurcation points in the underlying dynamics (h_{crit} and h_{erad} from the stoat equation alone, $h_{survival}$ from the coupled EGT–L-V system), and are not merely simulation artefacts (Supplement S1). Elasticity of kiwi population size to the four core L-V parameters (r, α, β, δ) collapses to near-zero at h=0.40 across all parameters simultaneously, while at h=0.15 the system is highly elastic (ε up to +41 for δ), confirming h=0.40 as an operationally robust policy target rather than a fragile threshold estimate (Supplement S2). All three thresholds remain within plausible bounds when stoat demographic parameters are varied across literature-derived ranges

(r_{stoat}=0.50-0.80, δ≈0.357), with uncertainty governed primarily by stoat demography and the behavioural (EGT) layer contributing negligibly. A wider stress test across the full non-mast r_{stoat} range (0.30-0.90) shows the h≥0.40 policy target is robust to moderate vital-rate uncertainty but may be insufficient during beech mast events, where r_{stoat} can rise to 1.5-2.5 (Supplement S3). Intervention timing has negligible effect at low harvest (h=0.16) but becomes consequential at intermediate harvest (h=0.20), where delay beyond ~year 17 prevents recovery to K_0 by t=200 (Supplement S4). Long-run recovery at h=0.40 is insensitive to both initial foraging strategy and behavioural adaptation rate across a 440-simulation joint sweep (Supplement S5).

Table 6. *Key Sensitivity and Robustness Outcomes*

Test	Parameter(s) / range swept	Key Result	Supplement
Bifurcation Analysis	Harvest rate h, full range	All 3 thresholds are exact bifurcation points, not simulation artefacts	S1
L-V parameter elasticity	r, α, β, δ at h=0.15/0.25/0.40	Elasticity → ~0 for all 4 parameters at h=0.40; extreme at h=0.15 (up to ε=+41)	S2
Threshold robustness	r_{stoat}=0.50–0.80, δ≈0.357	h_{crit} 0.14–0.44, h_{erad} 0.21–0.51, $h_{survival}$ 0.07–0.33; behavioural layer minor	S2
Mast-event stress test	r_{stoat} full non-mast span 0.30–0.90; mast r_{stoat}=1.5–2.5	h≥0.40 robust under non-mast; insufficient during mast events	S3
Intervention timing	Start year 0–30 at h=0.16, h=0.20	Negligible at h=0.16; matters at h=0.20 (fails if delayed past ~yr 17)	S4
Initial strategy / learning rate	$x_0 \in$ [5%,80%] (also [1%,99%]), $\kappa_{learn} \in$ [0.1,18.0], 440 sims	K(t=200) varies <2.2% of K_{max} across full joint grid	S5

Comparison with Observed Ecological Outcomes. The CEPPM's outputs are broadly consistent with observed ecological outcomes from New Zealand kiwi management programmes across three dimensions. Informal discussion with DOC's Predator Control team indicated general interest in decision-support tools of this kind for harvest control planning and operations, though systematic field validation remains outside the scope of this work. The absence of an interior coexistence equilibrium under unmanaged conditions matches the field-documented 2% annual kiwi decline (McLennan et al. 1996; DOC 2018), indicating this is a structural property of the system rather than a parameterisation artefact. The effective recovery threshold h≈0.165 is consistent with field experience from the Murchison Mountains programme, where a low-intensity landscape-scale stoat trapping network produced only marginal kiwi population recovery with chick survival rising from 19% to 37% and projected population growth shifting from -1.6% to +1.2% per annum (Tansell et al. 2016), reflecting stoat suppression insufficient to cross the effective recovery threshold. The h=0.40 target aligns with DOC's aerial 1080 outcomes where chick survival reached 60% in managed areas (Graham 2016), and Scenario 3a's recovery timescale (eradication within ~15 years, kiwi recovery over 60–80 years) broadly matches intensively managed sanctuaries, though direct comparison is limited by differing initial conditions and reinvasion pressure. The model's main divergences from field data are the optimistic eradication outcomes and its inability to represent mast-driven stoat irruptions, which follow from the structural limitations identified rather than parameterisation error and do not affect the qualitative conclusions.

Limitations

Several limitations bound interpretation. Structurally, the model requires payoffs to represent intra-generational utility rather than genetic fitness, an adaptation timescale commensurate with the population cycle, and a 2-strategy game on [0,1] over finite time. Extensions beyond these would need separate justification. It is parameterised for a closed, non-mast, ~1,000 ha sanctuary: it does not simulate beech-mast stoat irruptions (which can exceed modelled carrying capacity by an order of magnitude in a single season; Barlow & Barron 2005), stoat reinvasion from surrounding habitat, other predators (ferrets, cats, dogs), age/size-structured kiwi demographics, or the economic cost of control. Harvest thresholds should therefore be read as non-mast minimums, and eradication outcomes as potentially optimistic relative to open mainland sites.

Several parameters lack direct empirical support and were calibrated rather than measured: the payoff matrix, learning rate, and sigmoid penalty parameters (p_{open}, p_{cover}, k, S_{mid}, vulnerability weights) have no published kiwi-specific analogue and rely on sensitivity analysis as their primary defence. Two choices bias the model conservatively: S_{max}=8 yields a non-kiwi stoat floor (3.333/1,000 ha) below field estimates of 5-8 (Murphy & Dowding 1994, 1995), so harvest thresholds are likely conservative minimums; and r=0.05 reflects a managed rather than intrinsic growth rate, likely underestimating recovery speed. The death rate δ=0.35 may conflate natural and management-induced mortality (King 1983; Powell & King 1997), and harvest h is modelled as a constant rate rather than the pulsed structure of real operations. None of these limitations affect the model's central qualitative findings which are the absence of unmanaged coexistence and the existence of distinct harvest thresholds. These findings remain robust across the parameter ranges tested (see Sensitivity) and consistent with field programme outcomes.

Conclusion

We developed a Coupled Evolutionary Predator-Prey Model (CEPPM) that integrates replicator dynamics with an extended Lotka-Volterra framework to derive conservation policy implications for kiwi management. The model allows kiwi foraging strategy and population dynamics to co-evolve in response to stoat predation pressure, with payoff functions dynamically adjusted as a function of stoat density. Extensions to the standard framework include logistic kiwi growth, a predator saturation ceiling, and a generalised stoat equation that permits persistence on non-kiwi prey. Model parameters are empirically aligned with field data from New Zealand's conservation programmes and related studies.

Four principal findings emerge. First, the model identifies three distinct management thresholds for annual stoat removal: an effective kiwi recovery threshold $h_{survival}$≈0.165, below which kiwi extinction proceeds regardless of intervention timing; an analytical stoat suppression threshold h_{crit}=0.25, above which non-kiwi prey alone cannot sustain net stoat population growth; and a true stoat eradication threshold h_{erad}≈0.33, above which stoats are driven to eradication. Second, foraging strategy converges to different equilibria depending on scenario: ≈76% open foraging under full recovery, ≈65%-70% under partial recovery, and ≈44% under unmanaged conditions. Third, sensitivity analysis reveals that elasticity drops to near zero across all parameters at h=0.40, meaning this harvest rate provides genuine operational robustness to uncertainty in stoat vital rates, predation rate, and kiwi

growth rate simultaneously, substantially strengthening the case for h=0.40 as a minimum operational target. Lastly, the divergence between the simulated dynamic ESS (≈76%) and the survival-enabling foraging strategy (≈40.6%) illustrates that above the survival harvest threshold (h=0.165), increasing predator control progressively releases the population from the survival constraint, allowing replicator dynamics to drive open foraging toward the ESS and thereby accelerating demographic recovery. This mechanism is not visible through standalone demographic models.

The CEPPM contributes to the growing body of work coupling evolutionary game theory with predator-prey population mechanics (Křivan 2007; Cressman et al. 2004; Karmakar et al. 2025) by applying this framework to a specific, well-parameterised conservation system. The separation of behavioural adaptation and demographic change in existing models is shown to be not merely a simplification but a source of qualitatively incorrect predictions. The standalone EGT cannot distinguish a managed from an unmanaged population, and the standalone L-V model ignores the synergistic effect of behavioural compensation on demographic recovery. The effective kiwi recovery threshold is a finding that emerges only from the coupled model, and illustrates more broadly that management thresholds derived from single-component models may systematically underestimate the harvest intensity required for population recovery in systems where prey behaviour is adaptive. Key limitations are the restriction to intra-generational learned adaptation, exclusion of mast dynamics and spatial reinvasion, and several uncalibrated parameters. These are detailed above and do not alter the qualitative findings, which remain robust across plausible parameter ranges.

As New Zealand advances toward its Predator Free 2050 goal, quantitative frameworks that capture the full complexity of predator-prey interactions including the behavioural responses of threatened prey will be essential to identifying the management thresholds at which intervention becomes genuinely effective.

Acknowledgments

The authors wish to thank *Dr Anantanarayanan Thyagaraja* (Bristol University, UK) for a review of the research report and clarifying additional limitations of the model; *Dr Claire Postlethwaite* (University of Auckland) for literature recommendations, early feedback on the modelling approach and a review of the manuscript; *Matt Maitland* (Department of Conservation) for feedback on the decision support tool; and *Mrs Ghanim* and *Dr Steel* (Epsom Girls Grammar School) for support throughout this research. The authors also acknowledge the use of Claude (Anthropic, claude.ai) and Google Colaboratory (Google CoLab; colab.research.google.com) to aid with aspects of this research. Claude was used for iterative development of the software encoding of the model in Python, debugging of the simulation code and analysis scripts, literature search assistance, accuracy verification, and creation of an interactive webpage for demonstration. Google CoLab provided the cloud-based computing environment in which the simulation code was refined and executed. All model design decisions, parameter choices, graph design and visual representations, empirical interpretations, and final written content were verified, edited, and approved by the authors. The authors take full responsibility for the accuracy and integrity of all models, parameter estimations, results and conclusions presented.

Additional Information and Declarations

Author Contributions.

- SMS: Conceptualisation, Methodology, Validation, Formal analysis, Investigation, Data curation, Software, Writing – original draft, Writing – review & editing, Visualisation.
- NTS: Software, Writing – review & editing, Supervision.

Funding. This research received no external funding or financial support from any funding agency, institution, or commercial entity.

Data and Code Availability. The Python code for the Coupled Evolutionary Predator-Prey Model (CEPPM) and the analysis scripts used to generate the results in this study are openly available on GitHub at: https://github.com/nts-sms/CEPPM. The code is licensed under the MIT License.

Statement of Independent Research & Authorship. This research was conducted independently and outside of a formal institutional framework. The lead author (SMS) was responsible for the conceptual design of the Coupled Evolutionary Predator-Prey Model (CEPPM), the mathematical formulation of the extension and coupling of the replicator dynamics and Lotka-Volterra equations, parameterisation, analysis of results, and manuscript writing. The supporting author (NTS) contributed to software simulations and code management, literature sourcing, and manuscript review and editing. All parameters were sourced from publicly available, peer-reviewed ecological data and field reports. This manuscript is an original work and has not been influenced by any external commercial or institutional interests.

Conflict of Interests. The authors declare that there are no financial, personal, or professional relationships that could be construed as a conflict of interest or as having inappropriately influenced the representation or interpretation of the research reported in this manuscript.

Ethics Statement. Not applicable as no human or animal subjects were involved.

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Supplementary Material for Behavioural strategy and predator control: a coupled evolutionary predator-prey model for kiwi conservation in New Zealand (Authors: Sierra M. Sharma, Nagaja T. Sanatkumar)

Appendix S1. Bifurcation Analysis

We analysed four branches (A => Total extinction; B => Stoats survive, kiwi extinct; C => Full suppression of stoats; and D => Coexistence of both species) to examine if the system has sudden changes in response to continuous changes in harvest rates. We found that the three threshold harvest rates presented in Figure 3 (the recovery threshold h≈0.165, h_{crit}=0.25, and h_{erad}≈0.33) are not merely turning points observed in simulation but also correspond to bifurcation points in the underlying L-V equations. At each one, two of the model's possible long-term states meet and exchange stability (transcritical bifurcation at $h_{survival}$ from B⟶D, at h_{crit} between the unstable B and A branches which have already been dynamically superseded by D, and at h_{erad} from D⟶C). We confirmed this by tracking the eigenvalues of the system's Jacobian across the full range of harvest rates and found the coexistence state stable throughout its entire range, with no oscillatory instabilities emerging anywhere in between (Figure S1.1). h_{crit} and h_{erad} depend only on the stoat equation, so this result holds regardless of the EGT behavioural coupling. $h_{survival}$ depends on the EGT layer through the vulnerability-weighted optimal foraging strategy; stripping that layer out and using the Lotka-Volterra subsystem alone using fixed baseline r and α rather than their strategy-dependent forms reproduces a threshold within 0.06 percentage points of $h_{survival}$. Overall, the zone structure in Figure 3 rests on exact analytical grounding rather than simulation alone.

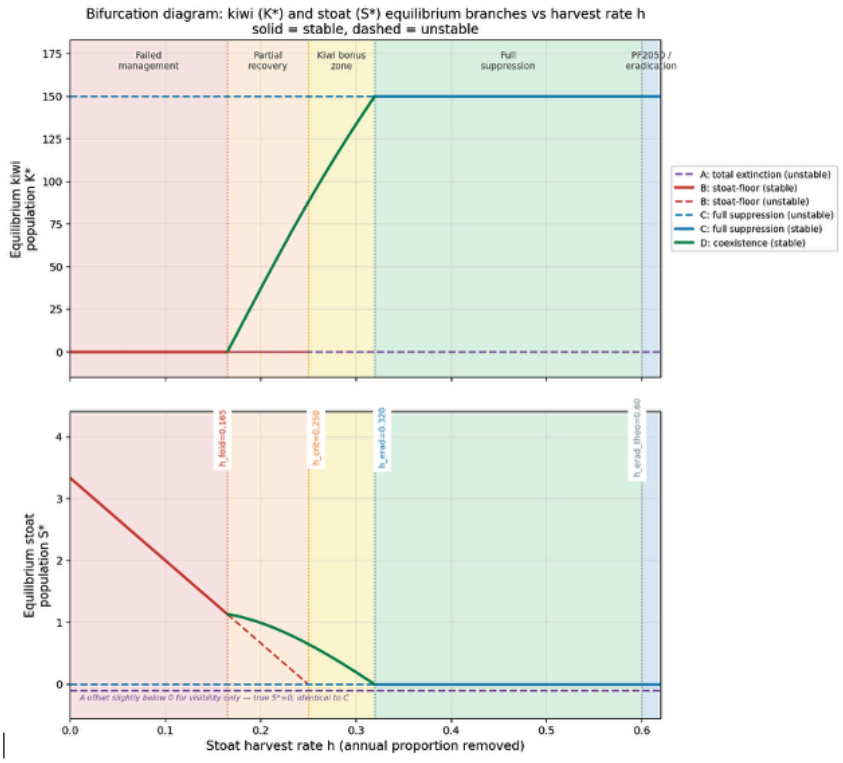


Figure S1.1. *2D Bifurcation Analysis*

Appendix S2. Parameter Elasticity & Threshold Robustness

Sensitivity of kiwi population K to variation in the four core L-V parameters was assessed by varying each across its plausible empirical range at three harvest rates, with intervention at year 20 (Table S2.1; Figure S2.1). The dominant pattern is not the elasticity value for any given parameter but its collapse across harvest rates: at h=0.40, elasticity approaches zero across all four parameters simultaneously (K remains near K_{max}=150 across the full plausible range of r, α, β, and δ) because stoat eradication removes predation regardless of parameter values. At h=0.15, by contrast, elasticities are extreme (ε=+9.32 for r, −11.89 for α, +41.1 for δ) reflecting the population's proximity to the extinction boundary, where small parameter shifts produce qualitative regime changes rather than incremental differences. At h=0.25 intermediate elasticities confirm that stoat suppression without eradication leaves the system sensitive to parameter uncertainty across all dimensions. The insensitivity of K to β across all harvest rates (ε≈0 at h=0.40, ε≈−0.31 at h=0.15) confirms that kiwi represent an ecologically negligible fraction of stoat diet, consistent with Murphy & Dowding (1995). The practical implication is that h=0.40 provides genuine operational robustness to parameter uncertainty that threshold-level management cannot match. This benefit does not appear in single-scenario analyses and that quantifiably distinguishes intensive from threshold management.

Table S2.1. *Summary of sensitivity coefficients of L-V parameters to kiwi population (K)*

Parameter	Range	h=0.15	h=0.25	h=0.40	Interpretation
r	0.02-0.20	+9.32	+0.59	+0.005	K increases with r; sensitivity collapses at h=0.40
α	0.01-0.10	-11.89	-0.87	-0.000	K decreases with α; irrelevant once stoats eradicated
β	0.005-0.050	-0.31	-0.60	-0.000	K insensitive to β; kiwi minor in stoat diet
δ	0.15-0.55	+41.01	+4.58	+0.001	K most sensitive to δ; sensitivity collapses at h=0.40

The model's baseline parameterisation (r_{stoat} = 0.60, δ = 0.35) yields $h_{survival}$ = 0.165, h_{crit} = 0.25, and h_{erad} = 0.33, taken as the central estimates throughout this paper. To assess robustness, we bound these estimates against literature-derived ranges for the governing stoat demographic parameters: r_{stoat} = 0.50–0.80 for non-mast podocarp/broadleaf forest (Barlow & Barron, 2005), and δ ≈ 0.357, corresponding to ~70% annual adult survival excluding management-induced mortality (Powell & King, 1997), which closely matches the baseline value. Across this range, h_{crit} varies from 0.14 to 0.44, h_{erad} from 0.21 to 0.51, and $h_{survival}$ from 0.07 to 0.33, with the baseline estimates falling within all three bounds (Figure S2.2). Sensitivity to the kiwi-predation-bonus parameters is asymmetric, and the pattern differs between thresholds. h_{erad} is relatively insensitive to the attack rate α (span 0.08) but more sensitive to the conversion efficiency β (span 0.18), reflecting β's direct linear role in $h_{erad} = h_{crit} + \beta \cdot f(K_{max},\alpha)$ versus α's saturating, sub-linear contribution via the Holling term. $h_{survival}$ shows the reverse pattern as it is comparatively more sensitive to α (span 0.19) and exactly invariant to β (span 0.00, since β only affects stoat dynamics once kiwi are already present in the coexistence state, while $h_{survival}$ governs the earlier invasion condition determining whether kiwi can begin recovering at all).

Extending the sweep to the EGT behavioural layer (payoff matrix a–d, vulnerability weights v_open/v_cover) and to the kiwi intrinsic growth rate r shows all of these are minor contributors to $h_{survival}$ (spans of 0.14 or less, most under 0.04), well below the stoat demographic parameters

(r_stoat span 0.42, δ span 0.36) or even α. Across all three thresholds, uncertainty is governed primarily by stoat demography, with the predation-bonus parameters playing a secondary, threshold-dependent role and the behavioural layer contributing negligibly. We therefore report h_{crit} ≈ 0.25 (range 0.14–0.44), h_{erad} ≈ 0.33 (range 0.21–0.51), and $h_{survival}$ ≈ 0.165 (range 0.07–0.33) as the recommended operational thresholds, rather than treating them as fixed point values.

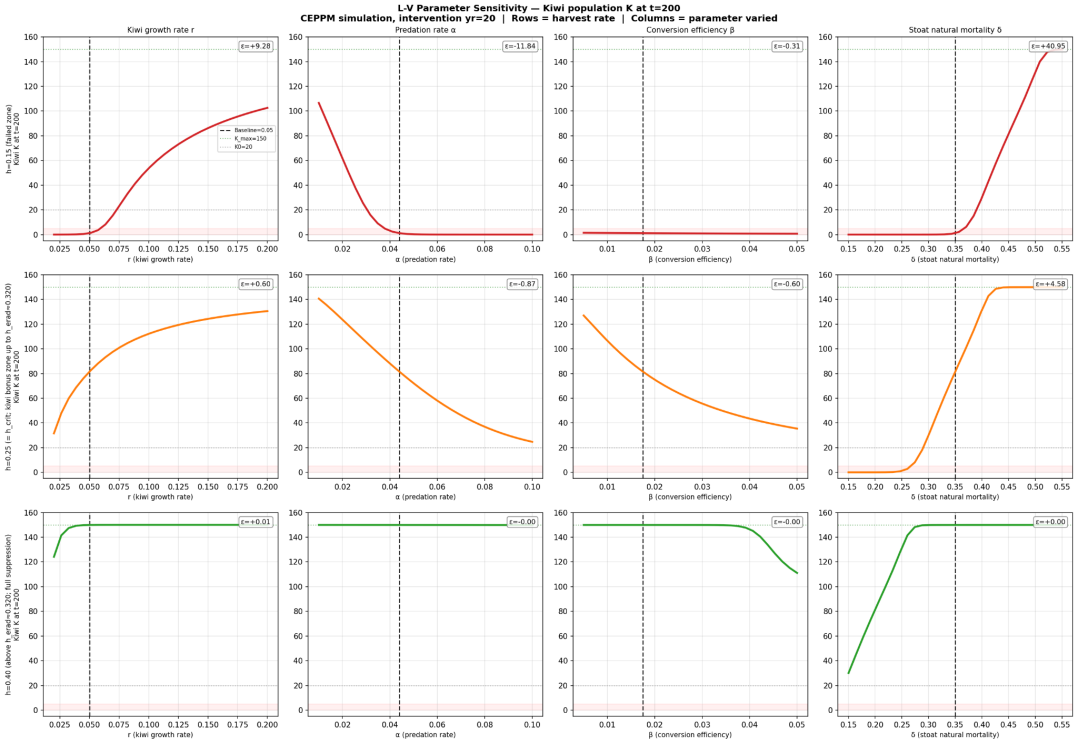
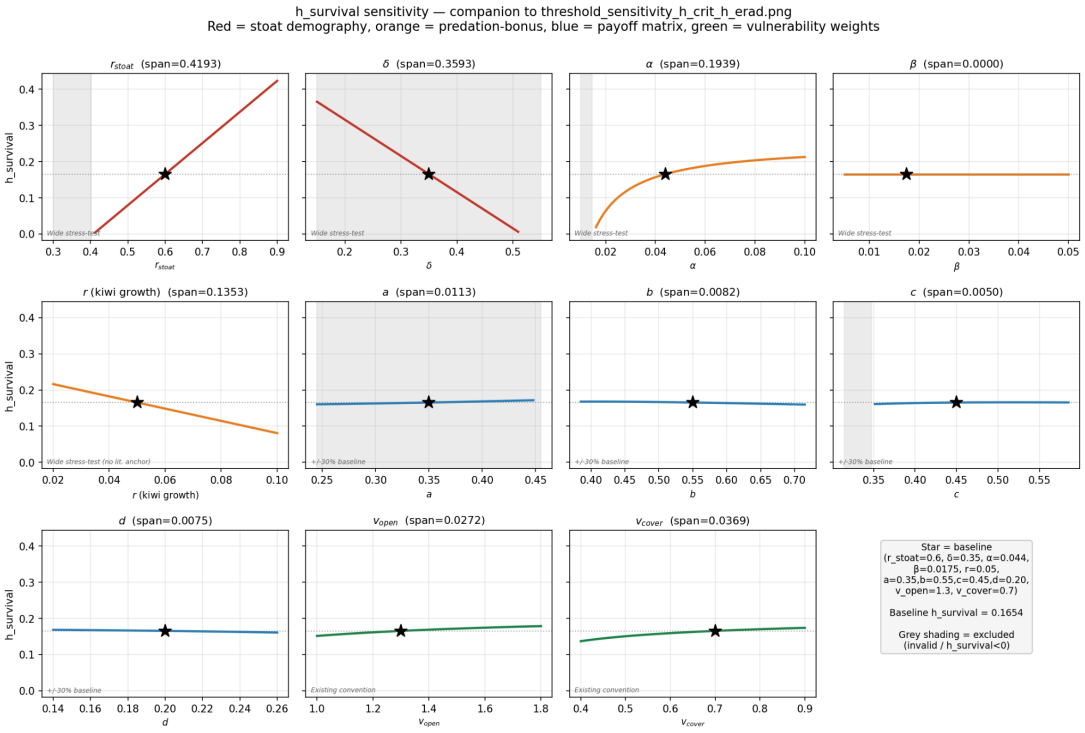
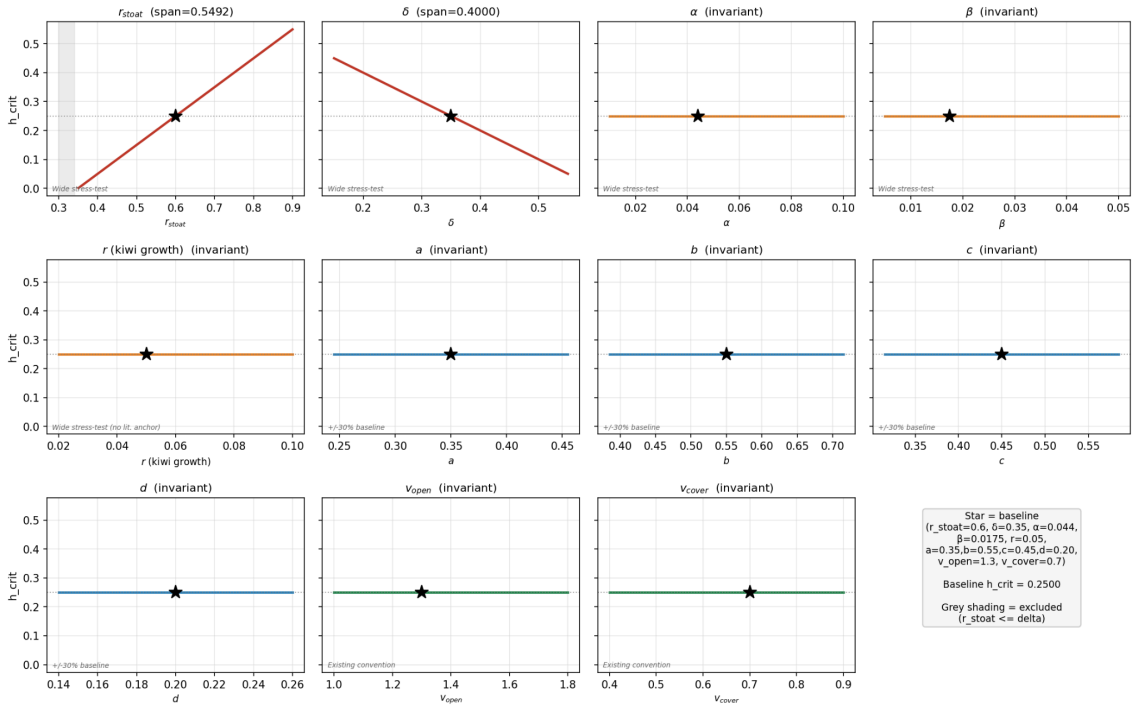


Figure S2.1. L-V Parameter Sensitivity vs Kiwi Population K


h_survival sensitivity — companion to threshold_sensitivity_h_crit_h_erad.png
Red = stoat demography, orange = predation-bonus, blue = payoff matrix, green = vulnerability weights
r_{stoat} (span=0.4193)
δ (span=0.3593)
α (span=0.1939)
β (span=0.0000)
r (kiwi growth) (span=0.1353)
a (span=0.0113)
b (span=0.0082)
c (span=0.0050)
d (span=0.0075)
v_{open} (span=0.0272)
v_{cover} (span=0.0369)
h_survival
Wide stress-test
Wide stress-test (no lit. anchor)
+/-30% baseline
Existing convention
Star = baseline
(r_stoat=0.6, δ=0.35, α=0.044,
β=0.0175, r=0.05,
a=0.35,b=0.55,c=0.45,d=0.20,
v_open=1.3, v_cover=0.7)
Baseline h_survival = 0.1654
Grey shading = excluded
(invalid / h_survival<0)


h_crit sensitivity — companion to threshold_sensitivity_h_survival.png
Red = stoat demography, orange = predation-bonus, blue = payoff matrix, green = vulnerability weights
r_{stoat} (span=0.5492)
δ (span=0.4000)
α (invariant)
β (invariant)
r (kiwi growth) (invariant)
a (invariant)
b (invariant)
c (invariant)
d (invariant)
v_{open} (invariant)
v_{cover} (invariant)
h_crit
Wide stress-test
Wide stress-test (no lit. anchor)
+/-30% baseline
Existing convention
Star = baseline
(r_stoat=0.6, δ=0.35, α=0.044,
β=0.0175, r=0.05,
a=0.35,b=0.55,c=0.45,d=0.20,
v_open=1.3, v_cover=0.7)
Baseline h_crit = 0.2500
Grey shading = excluded
(r_stoat <= delta)

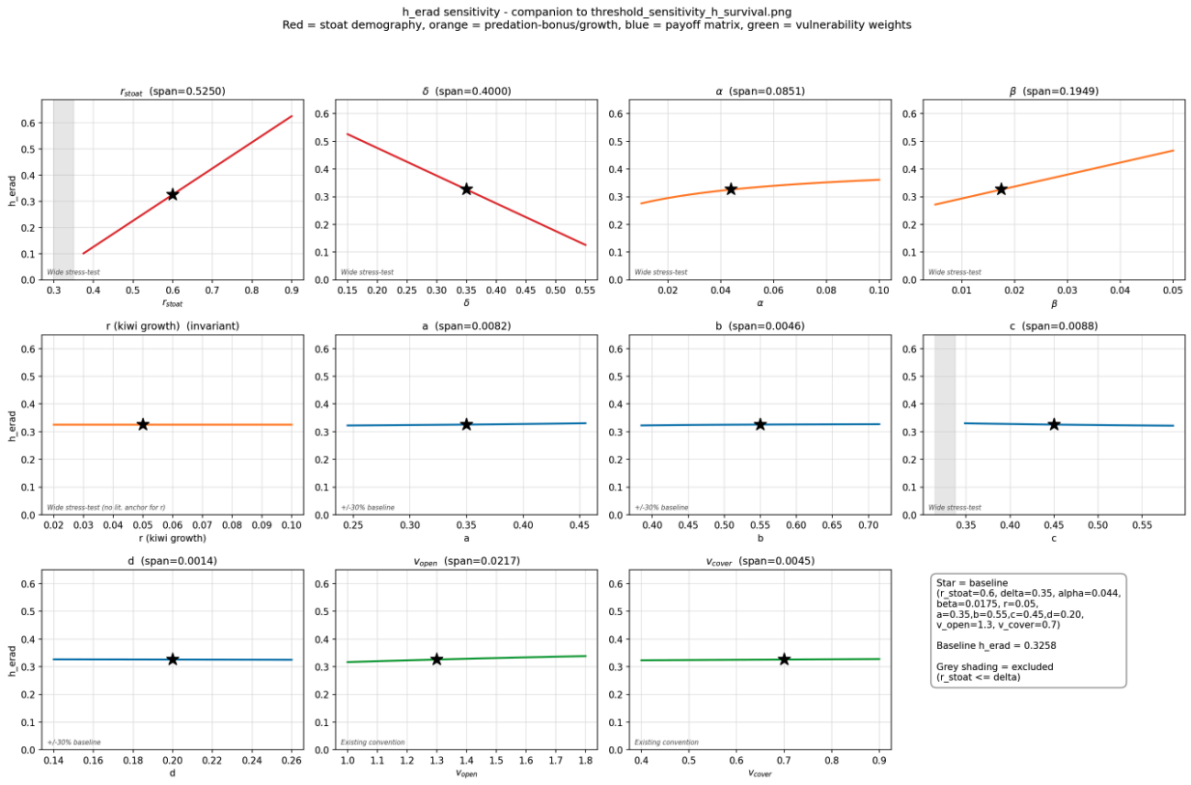


Figure S2.2. Sensitivity of $h_{survival}$, h_{crit}, h_{erad} to model parameters

The sensitivity analysis above establishes numerical robustness within the kiwi-stoat ecosystem, but there are structural conditions that establish the boundary of applicability to other systems. Generalising the model to other species pairs and/or different behavioural strategies is plausible as long as an interior ESS exists, and the ratio of the vulnerability weights either compensates or penalises a given strategy relative to the other. When the strategy favoured under declining predation pressure carries the higher vulnerability weight, the behavioural shift offsets demographic recovery (as in the kiwi-stoat case); when it carries the lower weight, the same mechanism reinforces recovery instead. These conditions can be tested and parameterised for other systems where the impact of capture on vulnerability under different behavioural states is known or can be estimated.

Appendix S3. Mast-Event Stress Test

As a further stress test beyond this literature-anchored range, we swept r_{stoat} across its full plausible non-mast span (0.30–0.90) using the 2D sensitivity maps below, which relate directly to management-relevant harvest rates. At baseline r_{stoat}=0.60, h=0.40 sits comfortably above h_crit=0.25. If r_{stoat} rises to 0.75, representative of productive non-mast conditions at the upper end of the Barlow & Barron (2005) range, h_{crit} itself rises to 0.40, meaning h=0.40 becomes the minimum rather than a comfortable margin above the threshold. Across the full swept range, the baseline parameterisation sits within the recovery zone at h=0.40 but on or near the regime boundary at h=0.25. During beech mast events, where r_{stoat} may reach 1.5–2.5, h_{crit} rises far above any harvest rate achievable by current management programmes, confirming that the model's thresholds apply specifically to non-mast baseline conditions and that supplementary management during mast years is a structural necessity the model cannot represent. The policy implication that management should target h≥0.40 is therefore robust to moderate vital rate uncertainty under non-mast conditions, but may be insufficient during mast events where r_stoat rises substantially.

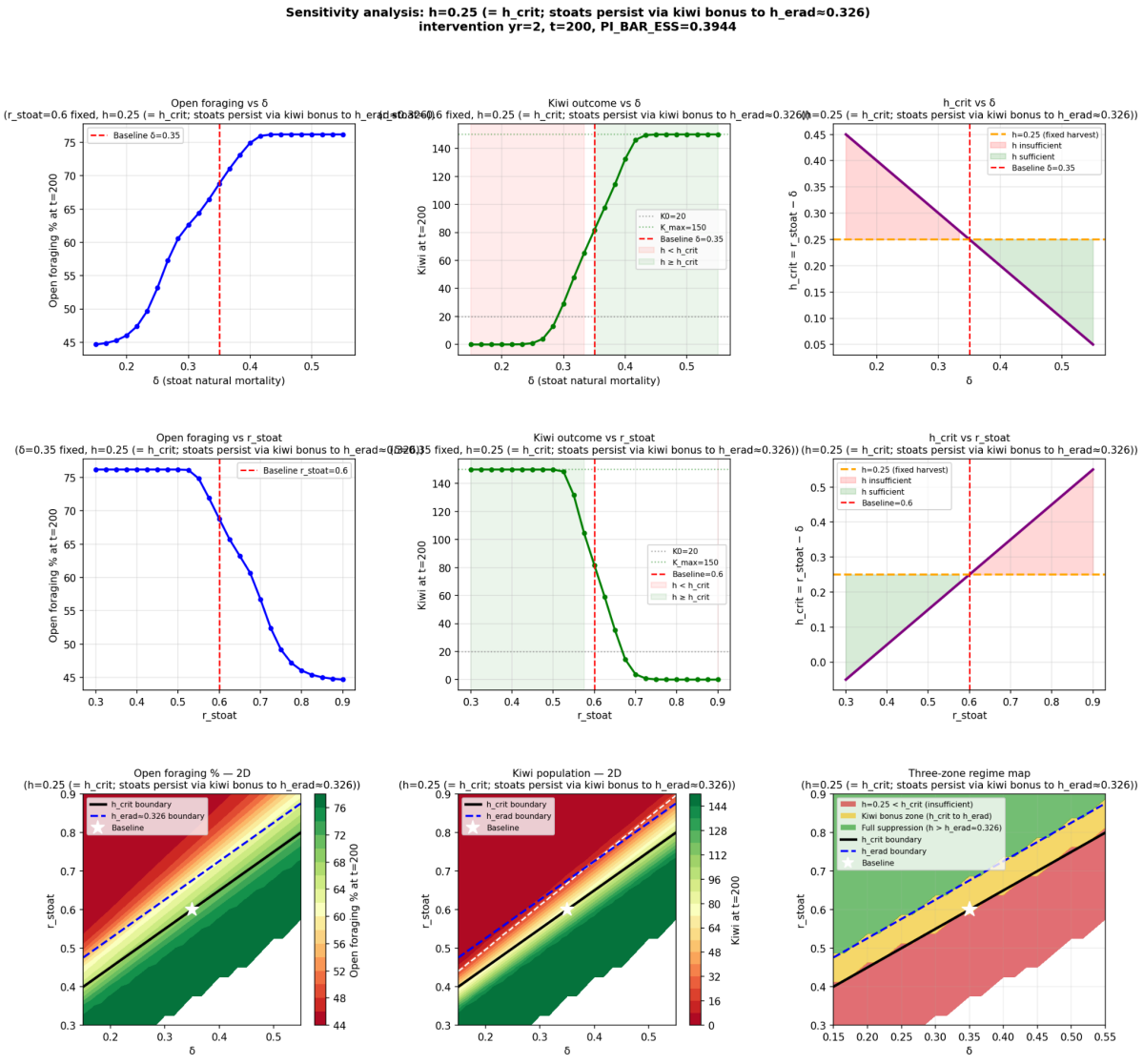


Figure S3.1. Sensitivity of h_{crit}=0.25 to stoat vital rates

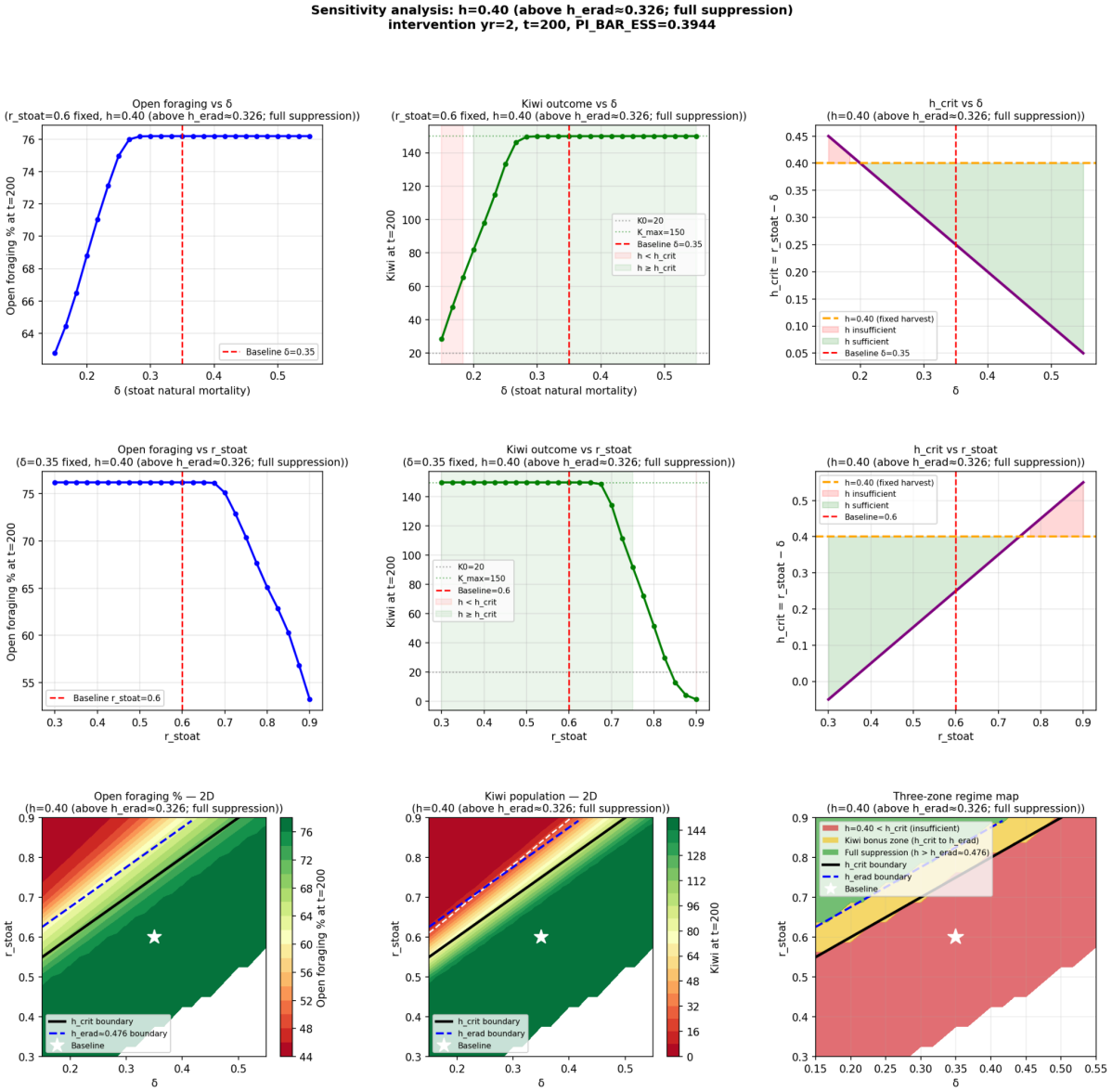


Figure S3.2. Sensitivity of h=0.40 to stoat vital rates

Appendix S4 — Intervention Timing Sensitivity

Intervention timing sensitivity was assessed at h=0.16 and h=0.20 across intervention years 0–30. At h=0.16, timing has almost no effect: K at t=200 ranges from only 3.9 to 0.6 across the full timing range, and stoats stabilise at S≈1.21 regardless of when management begins, because the harvest rate is insufficient to produce meaningful recovery irrespective of timing. At h=0.20, timing matters substantially for mid-term outcomes: K drops below K_0=20 if intervention is delayed beyond approximately year 17, meaning the population never recovers to its starting size by t=200. Together these findings reinforce that harvest rate is the primary management lever and that timing is a secondary consideration with meaningful but bounded consequences, and its relevance is contingent on the harvest rate being above the effective recovery threshold in the first place.

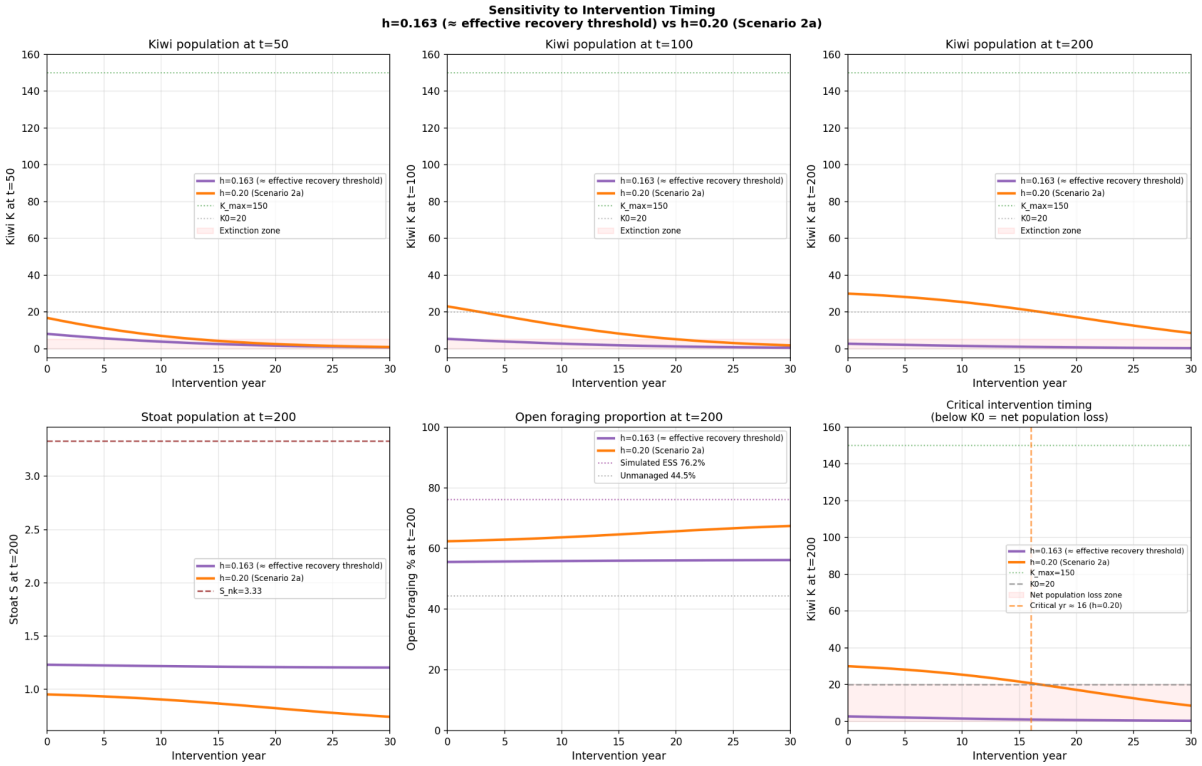
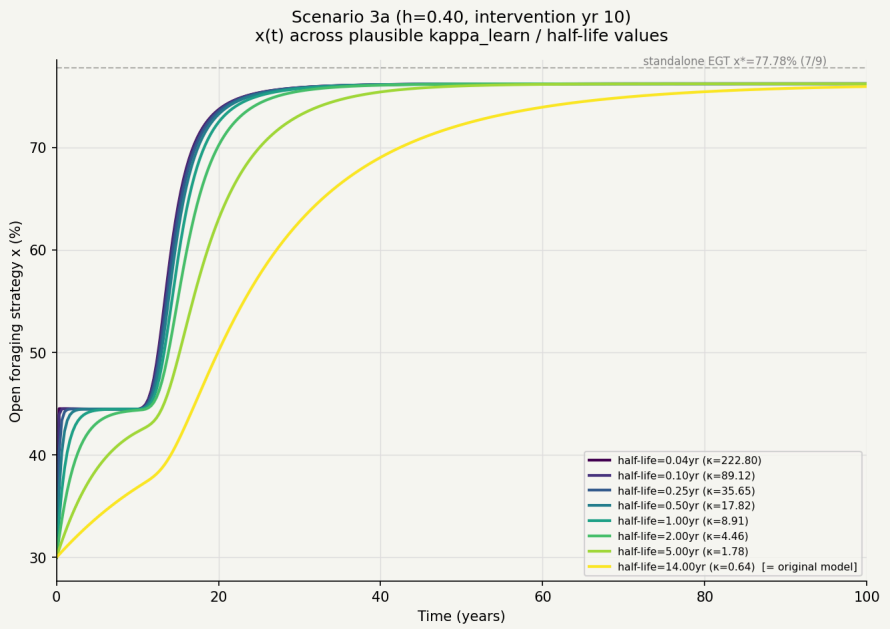


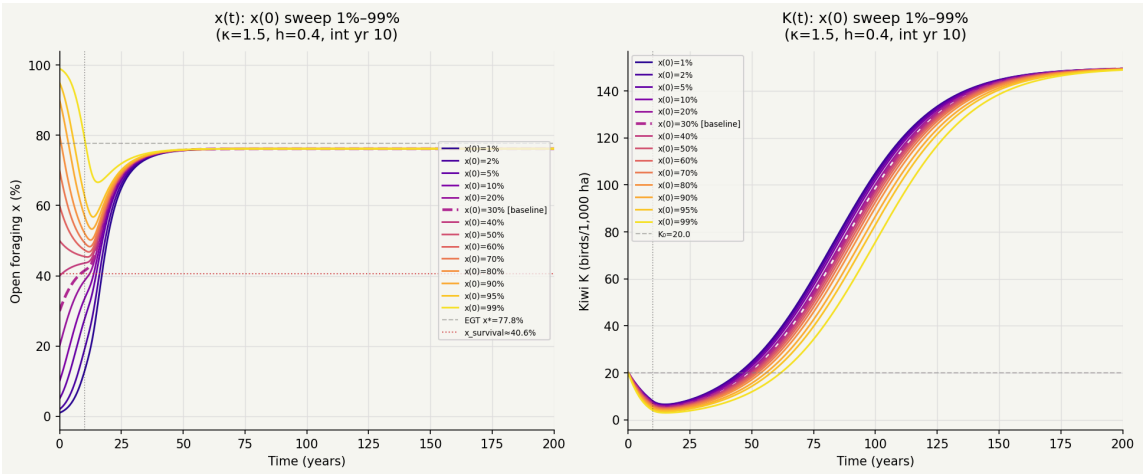
Figure S4.1. Sensitivity of intervention timing to CEPPM state variables

Appendix S5 — Initial Strategy & Learning Rate Robustness

Long-run kiwi recovery at h=0.40 is robust to both initial foraging proportion x_0 and behavioural adaptation rate κ_{learn}. Across $x_0 \in [5\%, 80\%]$ at baseline κ_{learn}=1.5/yr, K(t=200) varies by less than 0.6 birds, which is negligible relative to K_max=150. Even starting at x_0=5%, the system converges to x≈76% by t=100, confirming that the corner fixed points x=0 and x=1 are operationally unstable and trajectories are drawn toward the interior equilibrium regardless of starting position.

A joint 2D sweep across $x_0 \in [5\%, 80\%]$ and $\kappa_{learn} \in [0.1, 18.0]$ (440 simulations) confirms this simultaneously across both dimensions: K(t=200) ranges from 149.1 to 149.7 with standard deviation 0.05. Extending x_0 to the full [1%, 99%] range increases variation to 3.27 birds across the joint grid which is still less than 2.2% of carrying capacity, and concentrated in ecologically implausible corner cases combining near-zero κ_{learn} with extreme starting strategies. The model's long-run conservation conclusions at h=0.40 are therefore insensitive to uncertainty in both the initial behavioural state and the speed of strategy adaptation.





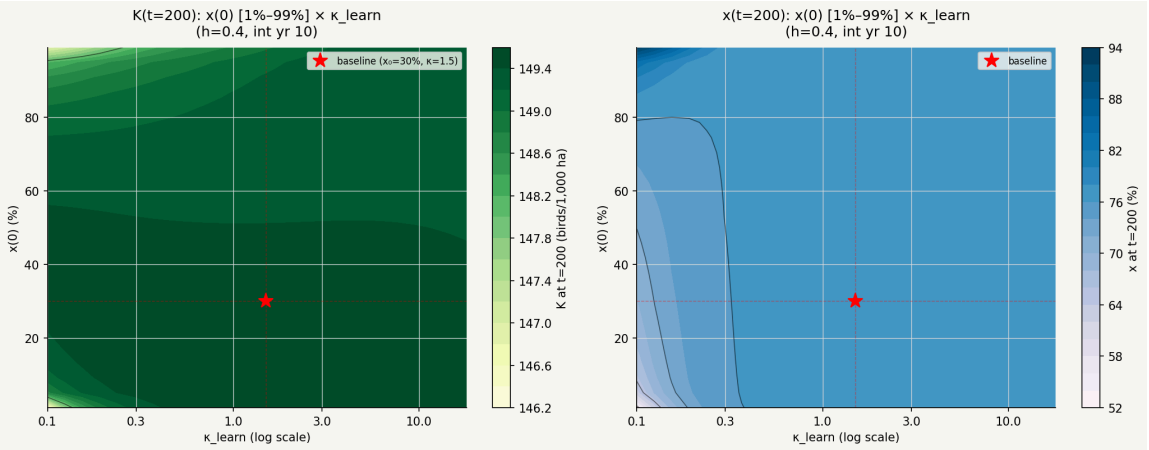


Figure S5.1. Sensitivity of kiwi population outcomes to Replicator Dynamic variables

Appendix S6 — Comparison of the CEPPM to EGT/L-V

Figure S6.1 compares simulation outputs across the three models for five scenarios. Three phenomena emerge that the standalone EGT and L-V models cannot replicate individually: scenario-dependent strategy divergence; identification of a 'survival-enabling' strategy boundary; and population divergence from L-V.

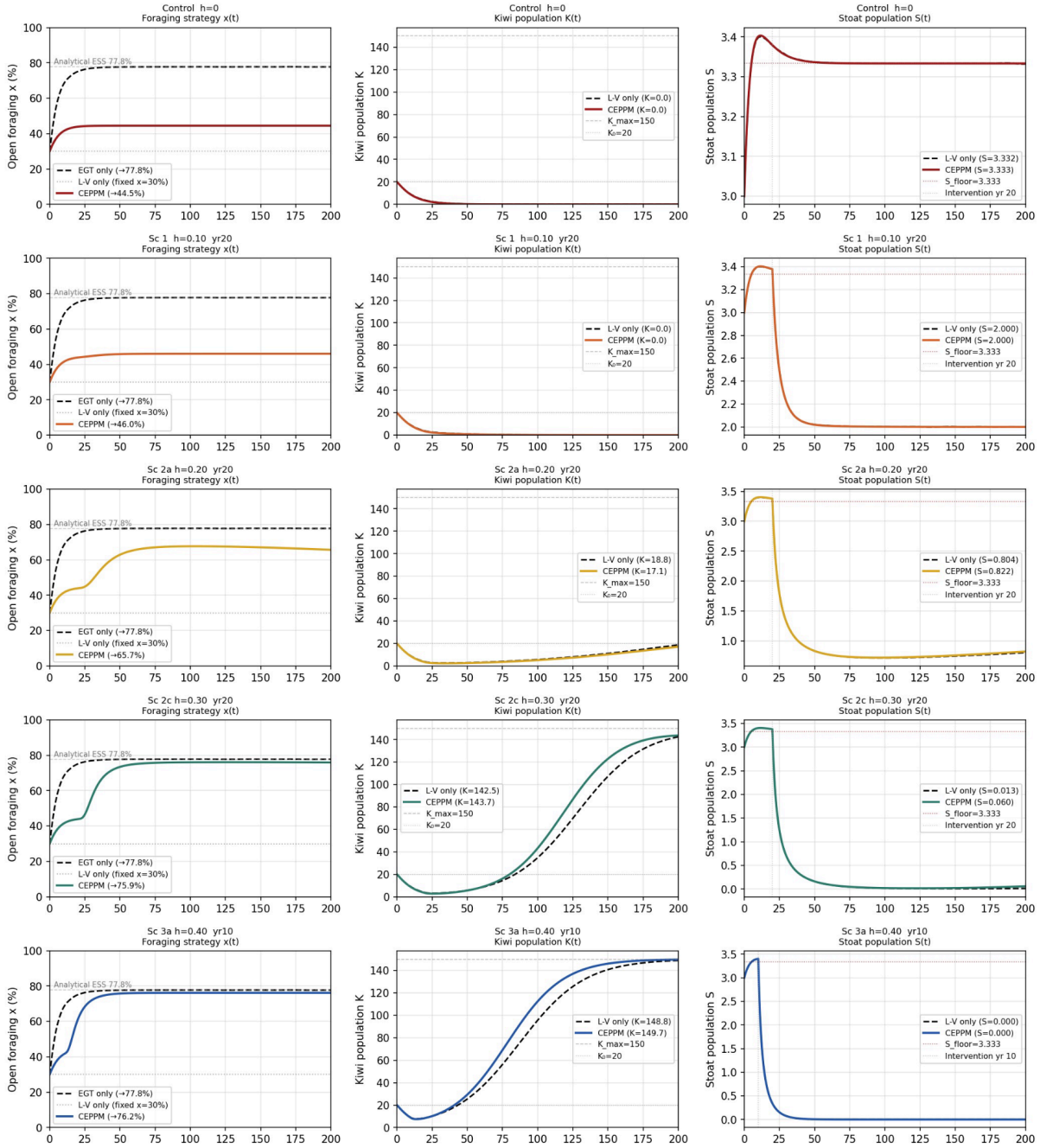


Figure S6.1. *Simulation outputs comparing the three models for five harvest scenarios*

The standalone EGT converges to the analytical ESS of x*=77.78% for all scenarios regardless of harvest rate or intervention timing, predicting identical equilibrium strategy whether stoats are eradicated or kiwi go extinct, because it has no mechanism to represent the ecological state. Open

foraging converges to ~76.2% in fully recovering scenarios where stoats approach eradication, approximately 76% in Scenario 2c where stoat density is minimal but non-zero, between ~65.7% and 69.6% in Scenarios 2a and 2b where partial stoat suppression persists, and remains suppressed near ~44-46% in extinction scenarios where stoat density remains at ecologically significant levels. The 1.58 percentage point gap between the CEPPM and analytical ESS in recovering scenarios arises from a residual sigmoid penalty at S≈0: even at near-zero stoat density the sigmoid function produces a small differential penalty on open foraging (≈0.0142) versus cover foraging (≈0.007), shifting the effective ESS below the analytical value computed from base payoffs alone. This is a qualitative consequential difference as standalone EGT cannot distinguish a managed from an unmanaged population, whereas the CEPPM's coupled payoff dynamics produce scenario-dependent equilibria that reflect the actual predation environment.

Minimum conditions for kiwi survival are analytically derived using Equations 10 & 11 with relevant parameter values.

$$C = \frac{r_{base}}{\alpha_{base} \cdot \bar{\pi}(x^*)} = 2.881 \; ; S_{critical} = 2.881 \cdot \max_{x \in [0,1]} \frac{\bar{\pi}(x)}{(0.7+0.6x)}$$

$$yielding\ x_{survival} \approx 0.406;\ S_{critical} \approx 1.128\ stoats\ per\ 1,000\ ha;\ h_{survival} \approx 0.1654$$

This derived survival harvest threshold (0.165) corroborates with the model's simulation sweeps that identify an effective kiwi recovery threshold at h≈0.163. A survival-enabling foraging proportion ≈40.6% is identified for kiwi to continue to recover (given this harvest rate and corresponding maximum stoat density of 1.128 stoats per 1,000 ha). The CEPPM simulated ESS at the same harvest rate yields ≈57% convergence at t=200. Increasing predator control above this harvest rate lowers the predation penalty, accelerates demographic recovery and drives open foraging towards the higher ESS of ≈76.2%.

The standalone L-V fixes strategy at x=30% throughout, treating kiwi as behaviourally static with constant parameters r and α derived from x_0=0.30. Under Scenario 3b this produces K=149.0 at t=200 versus the CEPPM's K=149.9, small but directionally consistent. Stoat dynamics also differ: in Scenario 2c, S=0.014 at t=200 under the L-V model while the CEPPM shows S=0.059. The CEPPM value is higher because the rising open foraging proportion increases α(x), providing slightly more kiwi predation that sustains stoats marginally longer through the kiwi bonus; at the simulated dynamic ESS=0.762, α(x*) is approximately 32% higher than at x0=0.30, since open foragers carry vulnerability weight 1.3 versus 0.7 for cover foragers. Hence the per-encounter predation rate is higher than the standalone L-V assumes. This increases kiwi mortality per stoat encounter through the f(α(x),K)·S term in the kiwi equation, while also marginally increasing the kiwi predation bonus in the stoat equation through β·f(α(x),K)·S. In practice this difference is negligible in recovering scenarios where stoats approach eradication regardless, but becomes more meaningful in partial-recovery scenarios where residual stoat density persists. The CEPPM reveals that as x rises toward the ESS, r(x) increases, amplifying kiwi growth, while α(x) also rises, partially offsetting this benefit through higher per-encounter predation risk. The net effect is positive and kiwi recover faster than the standalone L-V predicts, but the mechanism involves simultaneous and partially opposing behavioural effects that the coupled model captures and the standalone L-V cannot represent.

Appendix S7 — Supplementary Methods

Holling Type II saturation

The classic L-V model for the kiwi-stoat ecosystem allows the linear predation term αKS to scale without limit, resulting in the "atto-fox" problem. This occurs when a negligible predator population continues to exert predation pressure, resulting in catastrophic prey crashes at high prey density (Fowler, 2021).

$$\frac{dK}{dt} = rK - \alpha KS$$

The linear predation term αK is therefore replaced with the Holling Type II saturating functional response $f(K)$ (Holling, 1959) and resolves this problem by saturating predation at a ceiling of 1/H prey per predator per unit time. Holling's original disk equation includes an experimental time parameter T; setting T=1 gives the per-unit-time form used in the CEPPM.

$$f(K) = \frac{\alpha K}{1+\alpha HK}$$

$$\frac{dK}{dt} = r \cdot K \cdot (1 - \frac{K}{K_{max}}) - f(K) \cdot S$$

Unlike the attack rate α, which is already bounded against a literature range (0.01–0.10), the Holling Type II handling time H is fixed at H=0.1 throughout the paper, following Holling's (1959) mustelid parameterisation. Because $h_{survival}$ and h_{crit} are derived at K=0 and S=0 respectively, where the predation term f(K,H) either vanishes or drops out algebraically, both are exactly invariant to H. Only h_{erad} depends on H, through $\beta \cdot f(K_{max},H)$: as H ranges over its full mathematically permissible span (0 to ∞), $h_{erad}(H)$ is bounded between h_crit=0.25 (as H→∞, full predator satiation) and 0.384 (as H→0, no satiation at all). This span of 0.134 is comparable to the spans reported for r_{stoat} and δ. Critically, $h_{erad}(H)$ can never fall below h_{crit}, so the ordering $h_{survival}<h_{crit}<h_{erad}$ is preserved for every possible value of H, not merely across a plausible empirical range. Checked against the paper's three management scenarios (Table 5), this bound is never approached in practice: h=0.20 remains firmly in the light-management regime (partial kiwi recovery, stoats persisting) and h=0.40/h=0.60 remain firmly in the active-to-intensive regime (full stoat suppression) across the entire span of H, meaning the regime classifications reported throughout the paper are unaffected by uncertainty in this parameter.

Linear vs. sigmoid penalty comparison

Payoffs $\hat{\pi}$ are adjusted as a continuous function $\sigma(S)$ via a sigmoid penalty, where *k* is the sigmoid steepness parameter, S_{mid} is the sigmoid inflection point, and p_{open} and p_{cover} are the maximum possible penalties applied for open and cover foraging respectively (theoretical upper bounds when S →∞ and the sigmoid function →1). A linear penalty of the form p(S) = λS was considered, however this has no bound at high stoat densities, and does not account for diminishing marginal effects at the extremes. A sigmoid function has been used in other adaptive foraging studies (Křivan, 2007). This allows the payoff structure to mimic behavior that is ecologically consistent.

$$\sigma(S) = \frac{1}{1+e^{-k(S-S_{mid})}}$$

α(x)/r(x) offsetting-mechanism

The standalone L-V fixes strategy at x=30% throughout, treating kiwi as behaviourally static with constant parameters r and α derived from x_0=0.30. Under Scenario 3b this produces K=149.0 at t=200 versus the CEPPM's K=149.9, small but directionally consistent. Stoat dynamics also differ: in Scenario 2c, S=0.014 at t=200 under the L-V model while the CEPPM shows S=0.059. The CEPPM value is higher because the rising open foraging proportion increases α(x), providing slightly more kiwi predation that sustains stoats marginally longer through the kiwi bonus; at the simulated dynamic ESS=0.762, α(x*) is approximately 32% higher than at x_0=0.30 (the initial strategy), since open foragers carry vulnerability weight 1.3 versus 0.7 for cover foragers. Hence the per-encounter predation rate is higher than the standalone L-V assumes; open foraging kiwi are more vulnerable per encounter, and there are now more of them. This increases kiwi mortality per stoat encounter through the f(α(x),K)·S term in the kiwi equation, while also marginally increasing the kiwi predation bonus in the stoat equation through β·f(α(x),K)·S. In practice this difference is negligible in recovering scenarios where stoats approach eradication regardless, but becomes more meaningful in partial-recovery scenarios where residual stoat density persists. The CEPPM reveals that as x rises toward the ESS, r(x) increases, amplifying kiwi growth, while α(x) also rises, partially offsetting this benefit through higher per-encounter predation risk. The net effect is positive and kiwi recover faster than the standalone L-V predicts, but the mechanism involves simultaneous and partially opposing behavioural effects that the coupled model captures and the standalone L-V cannot represent. A behaviourally static model would attribute all demographic change to predator suppression alone and cannot represent the behavioural compensation effect that amplifies recovery when predation pressure falls.

ESS gap between EGT and CEPPM

The standalone EGT converges to the analytical ESS of x*=77.78% for all scenarios regardless of harvest rate or intervention timing, predicting identical equilibrium strategy whether stoats are eradicated or kiwi go extinct, because it has no mechanism to represent the ecological state. Open foraging converges to ~76.2% in fully recovering scenarios where stoats approach eradication, approximately 76% in Scenario 2c where stoat density is minimal but non-zero, between ~65.7% and 69.6% in Scenarios 2a and 2b where partial stoat suppression persists, and remains suppressed near ~44-46% in extinction scenarios where stoat density remains at ecologically significant levels. The 1.58 percentage point gap between the CEPPM and analytical ESS in recovering scenarios arises from a residual sigmoid penalty at S≈0: even at near-zero stoat density the sigmoid function produces a small differential penalty on open foraging (≈0.0142) versus cover foraging (≈0.007), shifting the effective ESS below the analytical value computed from base payoffs alone. This is a qualitative consequential difference as standalone EGT cannot distinguish a managed from an unmanaged population, whereas the CEPPM's coupled payoff dynamics produce scenario-dependent equilibria that reflect the actual predation environment.

Appendix S8. Full Parameter Justification

Parameters were sourced from the published New Zealand conservation and ecology literature wherever possible, prioritising primary field studies over modelled or aggregated estimates. Where direct empirical estimates were unavailable, values were derived from related demographic quantities or calibrated to produce qualitative behaviour consistent with empirically observed ecological thresholds, with the derivation process documented.

EGT Component Parameters

The payoff matrix accounts for three components: net food reward, a crowding cost reflecting kiwi territorial and solitary behaviour, and a predation-independent habitat comfort benefit applicable to cover foraging only. Open foraging yields a higher net food reward after accounting for greater travel costs at forest margins and higher vigilance time allocation in exposed habitat. Cover foraging carries an offsetting habitat comfort benefit reflecting predation-independent shelter value (Taborsky & Taborsky, 1995; Jamieson et al., 2016), and cover habitat reduces physiological stress costs associated with perceived exposure independent of actual predation mortality (Clinchy et al., 2013; Villén-Pérez et al., 2013). Crowding costs apply when both birds use the same habitat, reflecting competition for spatially limited foraging patches. Predation risk is handled entirely and explicitly by the sigmoid penalty term. Values are calibrated to produce an ecologically plausible interior ESS, directionally supported by literature, with sensitivity analysis as the primary quantitative defence.

Table S8.1. *EGT Component Parameters - Values and Justification*

Symbol	Value	Description	Basis for Assumption
a	0.35	Payoff to open forager meeting another open forager	Moderate reward reflecting intra-specific competition for exposed foraging sites
b	0.55	Payoff to open forager meeting a cover forager	Highest individual reward as open forager gains full food benefit when competitors forage elsewhere
c	0.45	Payoff to cover forager meeting an open forager	High reward as cover forager benefits from habitat comfort while open foragers do not
d	0.20	Payoff to cover forager meeting another cover forager	Lowest utility due to lower food reward and higher crowding costs
x_0	0.30	Initial proportion using open foraging	Conservative assumption reflecting high predation pressure in the absence of management
x*	0.7778	Analytical interior ESS	Derived: $x^* = (d-b)/[(a-b)+(d-c)] = -0.35/-0.45$; stable since $f'(x^*) = -0.07778 < 0$
κ_{learn}	1.5 /year	Behavioural adaptation or 'learning' rate	Not directly measurable; illustrative parameter anchored to documented sub-annual to multi-year habitat-use flexibility in the species (Dixon, 2015; Massaro et al., 2008). Robustness tested via sensitivity analysis.

Lotka-Volterra Component Parameters

L-V parameters are sourced from primary New Zealand field studies wherever possible. Kiwi demographic parameters derive from DOC monitoring data; stoat parameters from King (1983), Powell & King (1997), Murphy & Dowding (1994, 1995), and Barlow & Barron (2005). The predation rate α and conversion efficiency β are inferred from predation outcome and diet composition data.

Table S8.2. *L-V Component Parameters - Values and Justification*

Symbol	Value	Description	Justification
r	0.05 /yr	Kiwi intrinsic per capita growth rate	Conservative estimate representing managed rather than maximum biological rate. Department of Conservation (2018) Kiwi Recovery Plan suggests 2–5% recovery under active management.
α	0.044	Per capita predation rate constant	Derived at equilibrium: α = (r+0.02)/S* = 0.07/1.6; consistent with McLennan et al. (1996) predation outcome data[1]
β	0.0175	Stoat conversion efficiency from kiwi predation	Inferred from diet data[2]; kiwi <5% of stoat diet (Murphy & Dowding, 1995). Kiwi contribution to stoat growth negligible even at $K=K_{max}$
H	0.1	Holling Type II handling time	Consistent with Holling (1959) mustelid parameterisation. This parameter sets saturation ceiling of 1/H = 10 kiwi per stoat per year
K_0	20	Initial kiwi population per 1,000 ha	Consistent with baseline pre-management densities before sanctuary establishment (Department of Conservation 2018; McLennan et al., 1996)
K_{max}	150	Kiwi habitat carrying capacity per 1,000 ha	~1 bird per 6–7 ha, consistent with North Island brown kiwi territory size of 5–50 ha per pair (Robertson, 2013)
S_0	3	Initial stoat density per 1,000 ha	Represents pre-intervention site where stoat density has not yet reached non-kiwi equilibrium, hence below S_{floor}=3.333
r_{stoat}	0.60 /yr	Stoat intrinsic growth rate from non-kiwi prey	Consistent with Barlow & Barron (2005) fitted values of 0.50–0.80 for non-mast podocarp/broadleaf forest
S_{max}	8	Stoat carrying capacity from non-kiwi prey per 1,000 ha	Upper end of Murphy & Dowding (1994) home range estimates of 5–8 stoats/1,000 ha and within King & Powell (2007) range of 5–15 stoats/1,000 ha
δ	0.35 /yr	Stoat natural death rate (excludes harvest mortality)	Consistent with adult annual survival of ~70% from Powell & King (1997); explicitly excludes management-induced mortality

Derived Threshold Parameters

All threshold parameters are analytically derived from the L-V component parameters above, using CEPPM coupling where appropriate.

Table S8.3. *Derived Parameters - Value and Justification*

Symbol	Value	Description	Justification

[1] At equilibrium dK/dt = -0.02 (the unmanaged observed decline), so α.S*=r+0.02; at S*≡1.6 stoats/1000 ha, α=0.044

[2] Using an observed kiwi density of 20 birds/sq km gives β = δ/B* = 0.0175

S_{floor}	3.333	$S_{max}\cdot(1-\delta/r_{stoat})$	Non-kiwi stoat equilibrium at h=0. Stoat density sustained by rodents/invertebrates alone in absence of harvest
S*(h)	varies	$S_{max}\cdot(1-(\delta+h)/r_{stoat})$	Harvest-modified stoat equilibrium at rate h; declines linearly with h until $h=h_{crit}$
h_{crit}	0.25	$r_{stoat} - \delta$	Harvest rate at which S*(h) collapses to zero. Non-kiwi prey alone cannot sustain positive stoat population above this rate
$h_{survival}$	0.165	$r_{stoat}\cdot(1-S_{critical}/S_{max}) - \delta$	Effective kiwi recovery threshold as a new parameter that emerges from CEPPM dynamics, below which kiwi extinction proceeds regardless of intervention timing
h_{erad}	0.3258	$h_{crit} + \beta\cdot f(K_{max})$	Minimum harvest rate at which stoats are driven towards zero, calculated using CEPPM parameter values ($\alpha(x)$ evaluated at the CEPPM equilibrium x*, not the EGT x*)

CEPPM Parameters

These parameters define the sigmoid penalty function linking stoat density to foraging strategy payoffs. No published data exist on the stoat density at which kiwi foraging strategy distributions shift and hence values were chosen in line with ecologically feasible outcomes. The sigmoid curve has been calibrated such that the strategy transition from open to cover foraging occurs well below the empirically observed point where stoat predation drives kiwi chick survival to unsustainable levels.

Table S8.4. *CEPPM Component Parameters - Value and Justification*

Symbol	Value	Description	Justification
k	3.0	Sigmoid steepness	Penalty rises from 10% to 90% of maximum across ~1.5 stoats/1,000 ha, producing a gradual behavioural transition rather than an instantaneous switch
S_{mid}	1.0	Sigmoid inflection point (stoats/1,000 ha)	Sigmoid inflection point placed below unmanaged stoat densities at which stoat predation drives kiwi chick survival to 0–5% (McLennan et al. 1996), so that the strategy transition toward cover foraging is substantially complete before stoat density reaches levels causing severe demographic consequences (this occurs at approximately S≈1.5).
p_{open}	0.30	Maximum penalty applied to open foraging payoffs	Calibrated so adjusted ESS falls below x*=0.5 at S≈1.5 stoats/1,000 ha, reflecting greater vulnerability of open foragers
p_{cover}	0.15	Maximum penalty applied to cover foraging payoffs	Lower than p_{open} reflecting reduced predation exposure of cover foragers. The differential penalty drives strategy shift rather than absolute reduction
v_{open}	1.30	Open forager vulnerability weight	Assumed vulnerability ratio of ~1.86:1 between open and cover foragers, parameterised symmetrically around mean of 1.0
v_{cover}	0.70	Cover forager vulnerability weight	Complement to v_{open}; no kiwi-specific empirical measurements of strategy-differential predation mortality exist
π_{floor}	0.01	Minimum payoff floor	Ensures non-negativity of all adjusted payoff entries; no empirical basis; does not materially affect outcomes within ecologically relevant stoat density range

Simulation Settings

These are user-configurable, non-biological parameters that define the scenario being simulated. The values used in each scenario are reported in Results.

Table S8.5. *User-configurable Parameters*

Symbol	Description
T_{max}	Total simulation duration (years)
t*	Intervention year at which harvest h is activated; natural dynamics run for t < t*
h	Annual stoat harvest rate; proportion of stoat population removed per year through predator control

Structural Harvest Regimes

Table S8.6. *Possible Extended L-V model outcomes based on harvest rate vs. total stoat growth capacity*

Condition[3]	Predator Control	Stoat Dynamics
$h = 0$	No management	Stoats persist at $S^*_{full}(0) > S_{floor}$ sustained by non-kiwi prey and kiwi predation bonus
$0 < h < h_{crit}$	Light management	Stoats suppressed to positive non-kiwi equilibrium $S^*(h) = S_{max}\cdot(1 - (\delta+h)/r_{stoat}) < S_{floor}$. Full equilibrium marginally higher due to predation bonus.
$h = h_{crit} = r_{stoat} - \delta$	Stoat suppression threshold	Non-kiwi equilibrium $S^*(h_{crit}) = 0$; stoats may persist at positive equilibrium through kiwi predation bonus $\beta\cdot f(K^*)\cdot S$ as kiwi recover
$h_{crit} < h < h_{erad}$	Kiwi bonus zone	Stoats sustained at reduced positive equilibrium through kiwi predation bonus despite the non-kiwi equilibrium having collapsed to zero[4].
$h \geq h_{erad} = h_{crit} + \beta f(K_{max})$	Full suppression	Stoat eradication proceeds regardless of kiwi abundance
$h \geq r_{stoat}$	Intensive/PF2050	Theoretical upper bound where harvest exceeds total stoat intrinsic growth capacity

[3] Assuming a critical harvest threshold h_{crit} exists between 0 to 1.

[4] The full stoat equilibrium (including the kiwi predation bonus) reaches zero at $h \approx r_{stoat} - \delta + \beta\cdot f(K_{max})$, where K_{max} represents the kiwi carrying capacity toward which kiwi recover as stoats are suppressed. The difference between h_{crit} and h_{erad} reflects the kiwi predation bonus sustaining stoats at intermediate harvest rates. This represents a coupled feedback loop in which predator control enables kiwi recovery, which in turn partially sustains stoat populations through predation. Above h_{erad} stoat eradication is robust to kiwi abundance.

Appendix S9 - Glossary of Terms

Game Theory and Evolutionary Game Theory

Agent A decision-maker in a game (e.g. an individual, species, firm, or nation) assumed to act rationally in pursuit of maximising their own payoff.

Average payoff ($\bar{\pi}$) The proportionally weighted mean payoff across all strategies currently in use. In replicator dynamics, a strategy grows when its payoff exceeds the average payoff and declines when it falls below it.

Behavioural Adaptation Rate (κ_{learn}) The rate at which the population's collective foraging strategy adjusts in response to changing predation pressure. As stoat density rises or falls, the proportion of kiwi foraging in open habitat shifts accordingly. κ_{learn} determines how quickly this population-wide shift occurs.

Cooperative game A game in which players can form binding agreements or coalitions, potentially producing outcomes superior to those achievable through independent play.

Cover foraging (Strategy B) A kiwi foraging strategy in which birds feed under dense vegetation, reducing predation exposure at the cost of lower food intake. Modelled as the lower-fitness but lower-risk strategy relative to open foraging under high predation pressure.

Dominant strategy A strategy that produces a higher payoff than any alternative regardless of what other players do. In the Prisoner's Dilemma, defection is a dominant strategy for both players.

Evolutionarily Stable Strategy (ESS) A strategy that, once adopted by the majority of a population, cannot be successfully invaded by a rare mutant playing an alternative strategy. An ESS is a Nash equilibrium that additionally satisfies a stability condition: the incumbent strategy must do strictly better against a mutant than the mutant does against itself. Introduced by Maynard Smith & Price (1973).

Evolutionary Game Theory (EGT) The application of game theory to evolving biological populations, where strategies are inherited or imitated rather than consciously chosen, and payoffs represent reproductive fitness or utility outcomes. Strategy frequencies evolve over time according to replicator dynamics rather than deliberate optimisation.

Frequency dependence The property that the payoff of a strategy depends on how common it is in the population. A strategy may be advantageous when rare but disadvantageous when common.

Game theory The mathematical study of strategic decision-making among rational agents in competitive or cooperative environments. Concerned with predicting equilibrium outcomes given the structure of interactions and payoffs.

Hawk-Dove game A two-strategy game modelling conflict over a shared resource, where Hawks escalate and Doves retreat. The ESS is a mixed strategy with proportion V/C Hawks (resource value V, injury cost C). A foundational model in EGT.

Interior equilibrium An equilibrium at which both strategies coexist in the population at a proportion x* strictly between 0 and 1. May be stable (attracting) or unstable (repelling), depending on the sign of the derivative of the replicator equation at x*.

Nash equilibrium A strategy profile in which no player can improve their payoff by unilaterally changing their strategy, given the strategies of all other players. Every finite game has at least one Nash equilibrium (Nash 1950).

Open foraging (Strategy A) A kiwi foraging strategy in which birds feed in open areas, yielding higher food intake but greater exposure to stoat predation. Modelled as the higher-fitness but higher-risk strategy when predation pressure is low.

Pareto optimality An outcome is Pareto optimal if no player can be made better off without making another player worse off.

Payoff The fitness benefit (or cost) received by a player as a result of an interaction. In biological EGT (genetic evolution), payoffs represent reproductive success or survival probability. In behavioural EGT (learned adaptation), payoffs represent a utility outcome.

Payoff matrix A table of payoffs for all combinations of strategies across players. For a two-strategy symmetric game, entries a, b, c, d represent the payoff to the row player when facing each column strategy.

Player See Agent.

Prisoner's Dilemma A two-player game in which mutual defection is the Nash equilibrium even though mutual cooperation would produce higher payoffs for both players. Illustrates how individually rational decisions can produce collectively suboptimal outcomes.

Replicator dynamics A differential equation describing how a strategy frequency evolves over time in a large population. Strategies with above-average payoffs increase in frequency; those with below-average payoffs decline.

Strategy A complete plan of action for a player, specifying what to do in every possible situation. In EGT applied to the kiwi-stoat system, the two strategies are open foraging (Strategy A) and cover foraging (Strategy B).

Tragedy of the Commons The tendency for shared resources to be overexploited when individual users capture the full benefit of extraction but share the costs across all users. Each user's rational self-interest leads to collective resource depletion (Hardin 1968).

Predator-Prey and Population Dynamics

Atto-fox problem A pathological artefact of standard Lotka-Volterra models in which a vanishingly small predator population (e.g. 10^{-18} individuals) can still cause catastrophic prey crashes because predation scales linearly with prey abundance without saturation. Resolved by the Holling Type II functional response.

Carrying capacity (K_{max}) The maximum population size that a habitat can support given available resources. In the logistic growth model, the population converges to K_{max} in the absence of predation.

Coexistence equilibrium An interior equilibrium ($K^* > 0$, $S^* > 0$) at which both kiwi and stoat populations are stable.

Conversion efficiency (β) The proportion of energy gained from kiwi predation that is converted into stoat reproduction.

Critical harvest threshold (h_{crit}) The harvest rate at which the non-kiwi stoat equilibrium collapses to zero, derived analytically as $h_{crit} = r_{stoat} - \delta$. Below h_{crit}, stoats find a positive harvest-modified equilibrium $S^*(h) = S_{max} \cdot (1 - (\delta+h)/r_{stoat}) > 0$. At h_{crit}, this equilibrium reaches exactly zero. Note: above h_{crit}, kiwi contribution is insufficient to sustain stoats independently, so stoats decline to zero regardless of kiwi abundance.

Eradication threshold (h_{erad}) The minimum harvest rate at which stoats are driven toward zero regardless of natural mortality or prey availability.

Functional response The relationship between predator consumption rate and prey density. See Holling Type II functional response.

Generalised predator A predator whose population dynamics are not exclusively dependent on a single prey species.

Handling time (H) The time a predator spends pursuing, subduing, and consuming a single prey item. The key parameter in the Holling Type II functional response — larger H produces lower saturation ceiling 1/H.

Harvest term (h·S) The continuous proportional removal rate of stoats through predator control (trapping, 1080 etc.), modelled as h·S where h is the annual removal proportion and S is current stoat density. Bypasses the non-kiwi prey floor entirely such that sufficiently high h can drive stoats toward zero.

Holling Type II functional response A saturating predation function $f(K) = \alpha K/(1 + \alpha H K)$ that replaces the linear term αK in the standard Lotka-Volterra model. At low prey density it approximates linear predation; at high density it saturates at the ceiling 1/H, reflecting the constraint that a predator can only handle a finite number of prey per unit time regardless of availability (Holling 1959).

Kiwi growth rate (r) The intrinsic per capita growth rate of the kiwi population in the logistic equation.

Logistic growth A model of population growth in which the per capita growth rate declines linearly with population size, producing an S-shaped trajectory that converges to the carrying capacity K_{max}.

Lotka-Volterra equations A system of two coupled nonlinear differential equations describing predator-prey population dynamics. Prey grow logistically and are suppressed by predation; predators decline naturally and grow through prey consumption. The CEPPM extends these with logistic prey growth, Holling Type II predation, and a generalised stoat equation.

Natural mortality rate (δ) The per capita death rate of stoats from natural causes (starvation, disease, predation) excluding any management-induced mortality. Represents natural mortality only; predator control deaths using traps etc. enter separately through the harvest term h·S.

Non-kiwi prey floor See Stoat floor (S_{floor}).

Predation rate (α) The per capita rate at which a stoat encounters and attacks kiwi, expressed as a rate constant in the Holling Type II functional response.

Predator-prey dynamics The coupled oscillatory dynamics between a predator population and its prey, arising from the feedback between predation suppressing prey and prey availability driving predator growth.

Stoat carrying capacity (S_{max}) The maximum stoat population supportable from non-kiwi prey alone per 1,000 ha.

Stoat floor (S_{floor}) The stoat density at which growth from non-kiwi prey exactly balances natural mortality in the absence of harvest. Represents the stoat population that persists on rodents, invertebrates, and other birds even when kiwi are absent.

Stoat intrinsic growth rate (r_s or r_{stoat}) The maximum per capita rate of increase of the stoat population from non-kiwi prey, in the absence of management. Appears in the logistic growth term $r_{stoat} \cdot S \cdot (1 - S/S_{max})$ of the stoat equation, where it represents the maximum possible per capita growth rate from non-kiwi prey, realised only when stoat density is negligible relative to S_{max}. At higher densities the realised per capita growth rate is reduced by the factor $(1 - S/S_{max})$.

The Coupled Evolutionary Predator-Prey Model (CEPPM)

Base payoff matrix (Π) The fixed 2×2 matrix of utility payoffs for kiwi foraging strategies in the absence of predation pressure, used as the starting point before sigmoid penalties are applied.

Behavioural-demographic coupling The bidirectional feedback between strategy evolution (EGT component) and population dynamics (L-V component) in the CEPPM. High stoat density penalises open foraging payoffs → strategy shifts toward cover → effective predation rate α(x) falls → kiwi decline slows. Conversely, predator control reduces stoats → open foraging rewarded → higher r(x) → kiwi recover faster.

Coupled Evolutionary Predator-Prey Model (CEPPM) The full hybrid model developed in this paper, integrating replicator dynamics from EGT with an extended Lotka-Volterra predator-prey framework. State variables are x(t) (proportion of kiwi using open foraging), K(t) (kiwi population), and S(t) (stoat population). The three equations are fully coupled through dynamic payoff feedback and strategy-dependent L-V parameters.

Dynamic payoffs Payoff matrix entries adjusted in real time as a function of current stoat density S, via the sigmoid penalty function. Replace the fixed base payoffs in the replicator equation to create the behavioural-demographic coupling.

Effective growth rate r(x) The strategy-dependent kiwi growth rate in the CEPPM. As the proportion of open foragers increases, average payoff rises (up to a point) and effective growth rate increases. Open foraging produces higher food intake and therefore better reproduction when predation pressure is low.

Effective kiwi recovery threshold ($h_{survival}$) The harvest rate below which kiwi extinction proceeds regardless of intervention timing, identified analytically as $h_{survival} \approx 0.165$. Distinct from the analytical stoat suppression threshold $h_{crit}=0.25$, which is derived from the stoat equation alone. The effective kiwi recovery threshold is an emergent property of the coupled behavioural-demographic dynamics and cannot be derived analytically from either the EGT or L-V components in isolation. Its value depends on the full system including the dynamic payoff feedback, the strategy-dependent growth and predation rates, and the initial conditions. Between the effective kiwi recovery threshold and the stoat suppression threshold ($h_{survival} \approx 0.165$ to $h_{crit}=0.25$), kiwi survive but achieve only partial recovery, as stoats are suppressed but not eradicated.

Effective predation rate α(x) The strategy-dependent predation rate in the CEPPM. Open foragers are more exposed than average, cover foragers are less exposed.

Inflection point (S_{mid}) The stoat density at which the sigmoid penalty function $\sigma(S) = 0.5$ i.e. the midpoint of the range of penalty values affecting foraging strategy payoffs in response to stoat predation pressure.

Intervention time (t*) The year at which predator control begins in the two-phase simulation. Natural dynamics run for $t < t^*$; managed dynamics (with harvest rate h) run for $t \geq t^*$. User-configurable input.

Sigmoid penalty function (σ(S)) A logistic function $\sigma(S) = 1/(1 + e^{-k(S - S_{mid})})$ that maps stoat density S to a smoothly bounded value between 0 and 1. Used to scale the predation penalty applied to payoffs in the hybrid model. The sigmoid penalty reduces the payoffs of both strategies as stoat density increases, but applies a larger penalty to open foraging than to cover foraging. It is this differential (rather than an absolute reduction in either strategy's payoffs) that shifts the adjusted ESS toward cover foraging as predation pressure rises.

Strategy-dependent parameters The L-V model parameters r(x) and α(x) that vary with the current proportion of kiwi using each foraging strategy, creating the coupling from EGT to L-V in the CEPPM.

New Zealand Conservation Context

1080 (sodium fluoroacetate) A biodegradable toxin used in aerial and ground-based predator control operations in New Zealand. A single 1080 operation typically achieves 40–60% stoat knockdown.

Beech mast A periodic synchronised mass seeding event in southern beech (*Nothofagus spp*.) forests occurring every 3–5 years. Causes dramatic irruptions in rodent and stoat populations — stoat densities can exceed the model's S_{max} by an order of magnitude during mast years. Not explicitly modelled in the CEPPM, which represents a non-mast baseline.

Kiwi (*Apteryx spp.*) Five species of flightless, nocturnal ratite birds endemic to New Zealand, classified as threatened or at risk.

Predator Free 2050 New Zealand's national goal of eradicating stoats, rats, and possums from the mainland by 2050.

Stoat (*Mustela erminea*) An introduced mustelid predator, the primary driver of kiwi population decline in New Zealand. A generalist predator for whom kiwi represent less than 5% of dietary intake; population dynamics are primarily driven by rodent and invertebrate availability.
