EXERGY ANALYSIS OF A COMPLEX, MULTI-SPECIES EVOLUTIONARY HISTORY IN AN ISOLATED ECOLOGICAL NICHE

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ABSTRACT

This study extends an older two-species interaction model proposed by the same Authors a few years ago to describe three possible interaction modes (namely cooperative, parasitic and competitive) between different species. As in the previous model, we consider here a set of species occupying the same ecological niche but introduce a more complex interaction among the species. In the absence of predators, species N_1 (the "prey") would thrive in the assigned niche and -if undisturbed for a long period of time- reach its carrying capacity. The other species (three in this exercise) occupy the very same niche and display different interaction modes with the first one and among each other: N_2 and N_3 prey on N_1, N_3 preys also onN_2 while N_4 competes directly for N_1's food resources. We assume that the resources available within the niche can be quantified by their exergy content. Since the preys are also "resources" for the predators, they are assigned an exergy value proportional to the average calorific nutritional value of their meat.

The present study is more than a theoretical exercise in exergy resource allocation: it is intended to offer a contribution to a recovery plan prompted by a recent series of articles and news originating from the New Zealand Environmental Agency that described the situation of a critically endangered species,the Kākāpō (pronounced "ka·kuh·pow"), or *Strigops habroptilus*, a large, flightless, nocturnal parrot found only in New Zealand. It is the world's only flightless parrot, has a heavy build and nocturnal habits, is herbivorous with a low basal metabolic rate and a reported lifespan of up to 100 years. Originally preyed on by hawks and eagles, the Kākāpō developed a defensive strategy that allowed its survival over significant geological times. For several reasons the bird was exposed to new alien predators brought into its niche by humans in the last 1000 years or so and -unable to adapt- was on the verge of extinction until a conservation program was launched in the 2000. This is our species N_1. To simplify the treatment, we consider only two of Kākāpō's predators: stoats (N_2) and rats (N_3), both of which actively raid the nests and kill chicks. The competitor species (N_4) is the possum, who feeds on the same two- or three plant types as the Kākāpō.

After having quantified the resources, an evolution equation for each species is derived, and the behaviour of the 4 coupled equations is studied under a set of simplifying assumptions derived by the published field data. The resulting time evolution curves confirm that without strongly proactive conservation measures the Kākāpō would go extinct within few years and can only survive in environmental niches from which its "alien" predators have been eliminated. The model also provides an indication for the limit specific carrying capacity (individuals/km^2) and describes how this limit depends on the parameters of the model.

1 INTRODUCTION

In the last 120 years, the average abundance of native animal species in land-based habitats has fallen by at least 20%. About 40% of amphibian species, almost 33% of reef-forming corals and more than a third of all marine mammals are currently threatened. Even in the class "*Insects*", notoriously adaptable to environmental changes, the estimated rate of threatened species has increased to about 10%. Among vertebrates, the picture is still dimmer: at least 680 vertebrate species had been driven to extinction since the 16th century. A comprehensive analysis of the available evidence is offered by the IPBES 2020 Report by Brondizio et al (2019), in which the five direct drivers of change in nature with the largest relative global impacts so far are identified. In descending causal order: (1) changes in land and sea use; (2) direct exploitation of organisms; (3) climate change; (4) pollution and (5) invasive alien species. The Report also discusses a number of "remedies", i.e. of actions required to reach a more sustainable interaction among different environmental niches and suggests practical pathways for achieving them across and between sectors such as agriculture, forestry, marine systems, freshwater systems, urban areas, energy, finance and many others. Needless to say, the first and most important measure would be that of adopting integrated management and cross-sectoral approaches.

An example of a structured approach to the problem of endangered animal species entails several steps (not necessarily in the order listed below nor necessarily linked to each other):

1. Research and Identification
2. Habitat Conservation
3. Education and Anti-Overfishing/Overhunting Measures
4. Breeding Programs and Population Management
5. Research and Monitoring:
6. Community Involvement
7. Policy and Advocacy
8. International Cooperation
9. Long-term Sustainability
10. Adaptation and Flexibility/Resilience

The study presented in this paper falls under point (5): it is our belief that to better understand the ecology and biology of endangered species the on-the-field experimental investigations must be complemented by the development of suitable models that can monitor populations and track trends, assess the effectiveness of conservation efforts by comparing virtual scenarios and adapt strategies accordingly.

One of the main drivers of the evolution of a species in a given niche is the amount of resources it can avail itself of: specific boundary conditions like the interaction with possible predators may set an upper limit to the species numerosity, and the abundance or scarcity of preys may set an upper and a lower limit. But other types of interaction exist besides the "predator-prey" model: as discussed in detail in Sciubba & Zullo (2013) cooperation, specialization and parasitism play an important role in driving a species to reach the limit capacity of its niche or to extinction. As in our previous works, we adopt a Thermodynamic approach: assuming that the amount of resources can be quantified by their exergy, we argue that the time variation of the resource basis is directly linked to the numerosity of a generic species J. The presence of predators increases J's birth/mortality ratio, the presence of direct competitors for the resource basis reduces J's net input while the presence of possible preys increases it, and the presence of parasitic species reduces J's ability to capture and exploit the resources available in the niche.

The model discussed in this paper is a development and an extension of a one-species model first published in 2011 (Sciubba & Zullo 2011a) and 2011b)), in which we defined and quantified a "thermodynamically sustainable limit" for the numerosity of a species. In Sciubba & Zullo (2013) we presented an application of this exergy-based population model to a well-documented case of population de-growth, in Sciubba & Zullo (2014) we modelled the co-evolution of different species sharing common resources, and in Sciubba & Zullo (2012) we extended the model to include three different modes of interaction between two species.

In this paper, we analyse a more complex scenario, in which 4 species are present, two of which are predators and one a direct competitor of the species whose dynamics we want to assess.

The study has been prompted by a case that has received worldwide attention: the quasi-extinction of the Kakapo, a flyless parrot originary of New Zealand, that has almost eradicated in its original environmental niche by the introduction of new predators and of one direct competitor, all brought by humans on the islands.

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2 THE EVOLUTIONARY DRAMA OF THE KAKAPO

2.1 The Kakapo

The Kakapo is the world's only flightless parrot. It is indigenous to New Zealand and its name derives from the Māori word kākāpō, which means "night parrot." Its scientific name, Strigops Habroptilus, means "soft-feathered owl-faced". The parrot holds an important place in Māori history and folklore. These birds have very short stubby wings that they use only for support and balance. Since their wings do act as a parachute, Kakapos are adept at jumping from tree to tree, and to descend -somewhat clumsily- from the tree to the forest floor. Their foraging is mainly ground-based and takes place mostly at night. An adult bird measures about 50-60 cm in length and stands 30-40 cm high. It weighs between 2.5 and 5 kilos, with some males reaching 7: clearly the heaviest species of parrot in the world (Oldham, 2023). The kakapo, together with other parrot species, became isolated after New Zealand separated from Gondwana around 82 million years ago; and around 30 million years ago the kakapo diverged from the genus *Nestor* and in the process of adapting to terrestrial habits it probably started modifying its plumage color as well.

Figure 1: Kakapo adults and chicks

Kakapos are docile, curious and playful and do not shy away from human contact because they do not perceive them as predators. When alarmed, they stand upright to face their attacker.
With a lifespan extending up to 90 years, Kakapos are one of the longest-living species of birds in the world: this long life might be due to their relatively slow metabolism and their very low-energy intensive lifestyle. Kakapos have a sweet-musky odour that helps them find each other, but it also signals them to predators.

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The Kakapo was a thriving species throughout New Zealand well before the arrival of humans. They occupied various habitats (scrub- and temperate forest as well as coastal regions) while coexisting with the Maori population prior to the arrival of Europeans. Today, the only remaining Kakapo populations live on Codfish Island, Little Barrier Island, and Maud Island (Figure 2). In an attempt to save the species, researchers relocated also all remaining individuals from the mainland South Island to the offshore islands to save them from invasive species.

Some recent genetic studies conducted on both the remaining individuals and on the museum specimens (Atkinson & Merton, 2006) indicated that before the European colonization of New Zealand their numerosity might have been in the tens of thousands: while it is true that the Maori hunted the bird for food and plumage, their hunt was -characteristically for the Maori culture- somewhat “sustainable”: but they hunted with dogs, and introduced rats that ate eggs and killed chicks. When European settlers arrived, they brought even more invasive species like cats, stoats, and more rat species. The main indigenous predators of the Kakapo being hawks and harriers, the defensive strategy evolutionarily developed by Kakapos was to feed at night, stay on the ground and, when endangered, crouch down. This behaviour makes of course the task of hunters like cats, rats and stouts easier, and Kakapo populations quickly plummeted. True conservation efforts didn’t succeed until the late 1970s and 80s. Presently, there are only 215 Kakapo left (Bergner et al., 2016; Oldham, 2023)

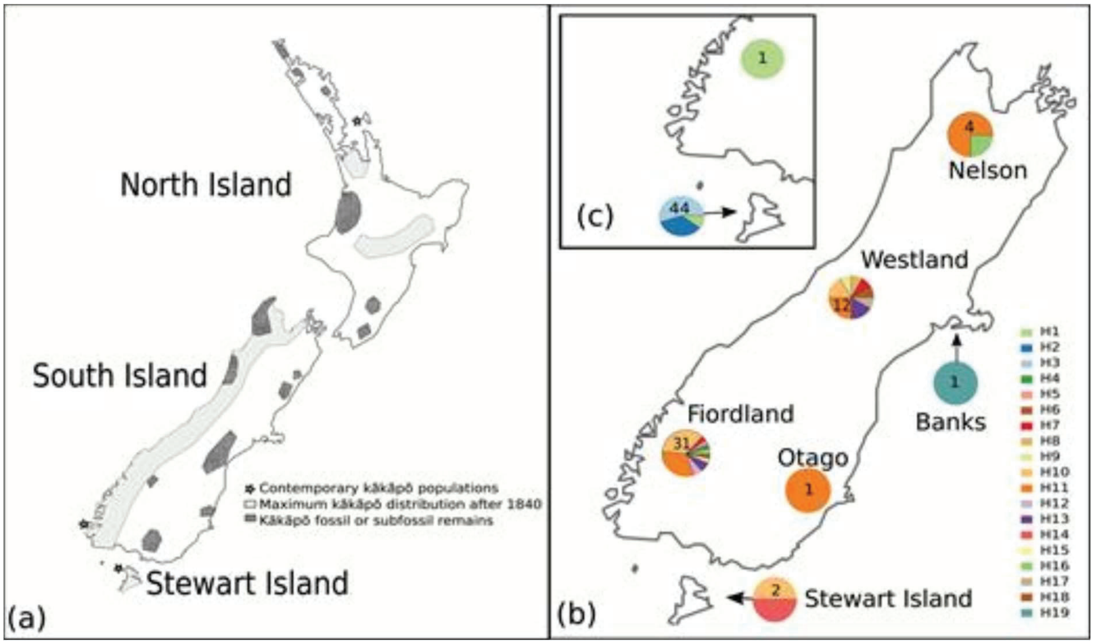

Figure 2: The historical (left) and current habitat of the Kakapo (adapted from Bergner et al., 2016)

The current adult Kākāpō population primarily descends from Stewart Island individuals relocated by conservationists in the 1990s, when their numerosity fell to 51 individuals. Extensive recovery actions were taken using tools such as planned matings and artificial insemination (to manage the risks of inbreeding and genetic drift) and led to a hitherto successful recovery.

2.2 - Diet of the Kakapo

Kakapos are herbivorous, with a very variable diet: they feed on fruits, nuts, berries, seeds, leaves, shoots, and even mosses and fungi when available: according to Atkinson & Merton (2006) they mainly forage on *Ribes rubrum* (Red Currant)*, Aciphylla takahea* (Spanish Grass)*, Schoenus pauciflorus (*bog rush)*, Podocarpus nivali (*a bushy conifer*), Polystichum vestitum* (Fern)*, Pseudopanax colensoi* (Mountain Five Fingers). . Even though they cannot fly, they do forage on trees and they are quite competent climbers.

2.3 - Predators and Competitors

As mentioned above, over several geological areas the kakapo encountered few natural predators in the wild and developed a suitable defensive strategy. But the first wave of Polynesian settlers brought rats and other nightly mammals that fed on vulnerable chicks left alone in their nest at night as the mother was off foraging. The arrival of European settlers completely transformed New Zealand's ecosystem with the reduction of the forest coverage and the introduction of cats, ferrets, and stoats. By the 1950s, the kakapo was almost completely extinct.

3 THE MODEL

Developing a model to describe the dynamics of an environmental niche that contains several preys or/and predators or/and competitors a difficult task, and its complexity grows with the number of species. Therefore, we chose to simplify the scenario as follows:

a) Kakapo is our target species N_1, i.e. the one whose dynamics we want to compare with experimental data;
b) Rats is the first predator species N_2. They eat chicks and eggs (rarely adult birds) but are in turn prey to Stouts. Their density (individuals/km^2) is high and assumed to be constant;
c) Stouts is the second predator species N_3. They are the top predator of our scenario, since they hunt even adult Kakapos and rats. Their density is lower than that of rats and also constant;
d) Possums is the competing species N_4, i.e. the one which directly competes with Kakapos for food. Their density is very high and their foraging much more effective than that of the Kakapo.

The assumption of a constant numerosity for N_2 and N_3 was introduced to make the mathematical treatment less impervious, but it also reflects a phenomenological feature of the environmental niche under observation: Stouts are pure carnivores and have several other sources of food (besides Kakapos, they eat eggs, lizards, rats, mice and passerines (Murphy et al., 2008)). Rats are omnivores and -besides Kakapos- eat insects, snails, frogs, lizards, birds and bats, but also flowers, fruits and seeds of plants. More importantly, Rats are fast breeders, making up for their falling prey to Stouts.

Define the growth rate of the population as the difference between the birth and death rates

$$\frac{\dot{N}(t)}{N(t)} = n - m \tag{1}$$

In our model, these rates are functions of the numerosity N and of the specific primary exergy consumption of the species. In Sciubba & Zullo (2011a) we have shown that the functions n and m can be determined by positing that:

a) If no limit is set to the availability of the resource (i.e., if the resource is infinite) then the population size is determined by the difference between its intrinsic birth (n_0) and death (m_0) rates;

b) If the availability of the resource drops to zero, so does the birth rate, while the mortality reaches a maximum (μ) that drives the population to extinction.

The two functions are given by Sciubba & Zullo (2011a)

$$n = \frac{n_0 \dot{E}}{\dot{E}+\sigma N}, \qquad m = \frac{m_0 \dot{E} + \mu\sigma N}{\dot{E}+\sigma N}. \tag{2}$$

Accordingly, equation 1) reads (Sciubba & Zullo (2011a)):

$$\dot{N}(t) = N(t)\left(\frac{r\dot{E}(t) - \mu\sigma N(t)}{\dot{E}(t)+\sigma N(t)}\right) \tag{3}$$

The constant σ represents the specific exergy consumption rate corresponding to a minimum survival: if the total energy consumption rate $\dot{E}$ is much greater than σN the population increases with a rate close to $n_0 - m_0$ whereas if $\dot{E} << \sigma N$ the population decreases with a rate close to μ. The generalization of equation (3) to Z interacting species reads

$$\dot{N}_i(t) = N_i(t)\left(\frac{r_i\dot{E}_i(t) - \mu_i\sigma_i N_i - \sum_{j\neq i}\chi_{ij}N_j(t)}{\dot{E}_i(t)+\sigma_i N_i + \sum_{j\neq i}\chi_{ij}N_j(t)}\right) \qquad i=1,2\ldots,Z \tag{4}$$

If species k preys on species j part of the corresponding exergy input $\dot{E}_k$ will be proportional to the numerosity N_j of the species j. Vice-versa, if species j is preyed upon by a species k, the corresponding coefficient χ_{jk} would be different from zero and represents a contribution to the mortality rate of species j: in fact, χ_{jk} can be considered a measure of the strength of competition between the two species (Sciubba & Zullo, 2011a).

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For reasons that will soon be clear, let us consider 4 species: in the absence of predators, species N_1 (the "prey") would thrive in the assigned niche and -if undisturbed for a long period of time- reach its carrying capacity. The other three species occupy the very same niche and display different interaction modes with the first one and among each other: N_2 and N_3 prey on N_1, N_3 preys also on N_2 while N_4 competes directly for N_1's food resources. The corresponding equations for the numerosities are given by:

$$\dot{N}_1(t) = N_1(t)\left(\frac{r_1\beta_1\dot{E}_1-\mu_1(\sigma_1 N_1(t)+\chi_{12}N_2(t)+\chi_{13}N_3(t))}{\beta_1\dot{E}_1+\sigma_1 N_1(t)+\chi_{12}N_2(t)+\chi_{13}N_3(t)}\right) \tag{5a}$$

$$\dot{N}_2(t) = N_2(t)\left(\frac{r_2\left(\dot{E}_2+p_{2,1}N_1(t)\right)-\mu_2(\sigma_2 N_2(t)+\chi_{23}N_3(t))}{\dot{E}_2+p_{2,1}N_1(t)+\sigma_2 N_2(t)+\chi_{23}N_3(t)}\right) \tag{5b}$$

$$\dot{N}_3(t) = N_3(t)\left(\frac{r_3\left(\dot{E}_3+p_{3,1}N_1(t)+p_{3,2}N_2(t)\right)-\mu_3\sigma_3 N_3(t)}{\dot{E}_3+p_{3,1}N_1(t)+p_{3,2}N_2(t)+\sigma_3 N_3(t)}\right) \tag{5c}$$

$$\dot{N}_4(t) = N_4(t)\left(\frac{r_4\beta_4\dot{E}_1-\mu_4\sigma_4 N_4(t)}{\beta_4\dot{E}_1+\sigma_4 N_4(t)}\right) \tag{5d}$$

As for the meaning of the many parameters appearing in equations (5a-5d):

a) Species N_1 and N_4 compete for their food, i.e. for their exergy input E_1. N_1 takes a fraction equal to β_1 of E_1, whereas N_4 takes a fraction equal to β_4. We assume that the allocation of the exergy flows at N_1 and N_4 increases with the numerosity of the respective population. So we set $\beta_1 = \frac{\gamma_1 N_1}{\gamma_1 N_1+\gamma_4 N_4}$ and $\beta_4 = \frac{\gamma_4 N_4}{\gamma_1 N_1+\gamma_4 N_4}$, (both in kJ/individual/day) that represent the specific exergy consumptions of the two species (notice that $\beta_1+\beta_4=1$). In principle the parameters γ_i could depend also on time: let us assume, for simplicity, that they are just constants;

b) N_4 has no predators and σ_4 measures its minimum specific exergy consumption rate, as σ_i for the other N_i's;

c) The parameter χ_{ij} represents the strength of competition between N_i and N_j;

d) As for N_2 and N_3: in the exergy terms in the numerator of eqtns. (5b) and (5c) multiplied by r_2 and r_3 we inserted, respectively, $N_1$and (N_1, N_2). Indeed N_1 represent a contribution (as food) to the exergy input to N_2 whereas both N_1 and N_2 provide an extra exergy input (again as food) to N_3;

e) The constants $p_{i,j}$ provide the conversion of the mass of the prey j into exergy utilized by the predator i. These are not the only exergy inputs to N_2 and N_3: the overall balance is closed, respectively, by $\dot{E}_2$ and $\dot{E}_3$.

3.1 An instantiation of the model

A complete analytical characterization of the system of equation (5a-5d) is an arduous task. Let us start by noticing that the set $F = \{N_1 > 0, N_2 > 0, N_3 > 0, N_4 > 0\}$ is an invariant submanifold for the system of equations: if the initial conditions belong to F, the corresponding solution remains in this set. Also, we take a specific, particular case of the system of equations (5a-5d): we assume that the numerosities of the predators, i.e. the species N_2 and N_3, are constant in time. This is a realistic approximation in many circumstances. For example, if the exergy flow to the species N_2 and N_3 are much greaterthan $p_{2,1}N_1(t)$ and $p_{3,1}N_1(t)$ -i.e. than the exergy flow coming to N_2 and N_3 from the species $N_1(t)$, then it can be shown that the steady states for N_2 and N_3 are given by the constant values with a degree of approximation that tends to zero (i.e., becomes exact) if $p_{2,1}N_1(t)$ and $p_{3,1}N_1(t)$ are zero:

$$N_2 \approx \frac{\sigma_3\mu_3 r_2 E_2-\chi_{23}\mu_2 r_3 E_3}{\mu_2(\sigma_2\sigma_3\mu_3+\chi_{23}p_{3,2}r_3)};\quad N_3 \approx \frac{r_3\left(p_{3,2}r_2 E_2+\sigma_2\mu_2 E_3\right)}{\mu_2(\sigma_2\sigma_3\mu_3+\chi_{23}p_{3,2}r_3)} \tag{6}$$

The effect of the global, constant term $T = \chi_{12}N_2 + \chi_{13}N_3$, appearing in equations (5a), is to decrease the value of the derivative of $N_1(t)$:

$$\dot{N}_1(t) = N_1(t)\left(\frac{r_1\beta_1\dot{E}_1-\mu_1(\sigma_1 N_1(t)+T)}{\beta_1\dot{E}_1+\sigma_1 N_1(t)+T}\right) \tag{7a}$$

$$\dot{N}_4(t) = N_4(t)\left(\frac{r_4\beta_4\dot{E}_1-\mu_4\sigma_4 N_4(t)}{\beta_4\dot{E}_1+\sigma_4 N_4(t)}\right) \tag{7b}$$

Equations (7a) and (7b) represent a shrunk system with respect to (5a-5d) and its analysis is more manageable. There are three fixed points, listed in Table 1.

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Table 1: The three fixed points for the system of equations (7a-7b)

	N_1	N_4
a)	0	$\frac{r_4\dot{E}_1}{\sigma_4\mu_4}$
b)	$\frac{r_1\dot{E}_1-\mu_1 T}{\sigma_1\mu_1}$	0
c)	$\frac{\gamma_4\mu_1 r_4 T}{\sigma_4\gamma_1\mu_4 r_1-\sigma_1\gamma_4\mu_1 r_4}$	$\frac{r_4 E_1}{\sigma_4\mu_4}-\frac{\gamma_1\mu_1 r_4 T}{\sigma_4\gamma_1\mu_4 r_1-\sigma_1\gamma_4\mu_1 r_4}$

Notice that we are considering solutions in the invariant submanifold $F=\{N_1>0, N_2>0, N_3>0, N_4>0\}$ and it is not guaranteed that for arbitrary choices of the constants of the model the fixed points (a-c) in Table 1 are always present in the first quadrant of the plane (N_1, N_4). For example, point b) is in the first quadrant of the plane (N_1, N_4) iff $\dot{E}_1 > \frac{r_1 T}{\mu_1}$, i.e. if the exergy input to the species N_1 (or N_4) is greater than a threshold value determined by the "competition exergy" T. For point c), the constants $\frac{r_1\gamma_1}{\mu_1\sigma_1}$ and $\frac{r_4\gamma_4}{\mu_4\sigma_4}$ play a crucial role: they represent a measure of the efficiency of the species to gain net exergy flows, which depends on the constants γ_1 and γ_4, on their specific exergy consumption rate corresponding to a "minimum survival", given by σ_1 and σ_4 and on the ratio of the growth rate to the mortality rate $\frac{r_k}{\mu_k}$ in the respective limit cases of infinite and zero resources available. Indeed, the pair $\left(\frac{\gamma_4\mu_1 r_4 T}{\sigma_4\gamma_1\mu_4 r_1-\sigma_1\gamma_4\mu_1 r_4}, \frac{r_4 E_1}{\sigma_4\mu_4}-\frac{\gamma_1\mu_1 r_4 T}{\sigma_4\gamma_1\mu_4 r_1-\sigma_1\gamma_4\mu_1 r_4}\right)$ is in the first quadrant if two conditions are satisfied:

- ✓ $\frac{r_1\gamma_1}{\mu_1\sigma_1} > \frac{r_4\gamma_4}{\mu_4\sigma_4}$
- ✓ $\dot{E}_1 > \frac{d_4\mu_4\gamma_4}{r_4\gamma_1} N_1^*$ where $N_1^* = \frac{\gamma_4\mu_1 r_4 T}{\sigma_4\gamma_1\mu_4 r_1-\sigma_1\gamma_4\mu_1 r_4}$

The first condition establishes that the value of N_1 given by c) in Table 1 is in the first quadrant if the overall parameter $\frac{r_1\gamma_1}{\mu_1\sigma_1}$ of N_1 is greater with respect to $\frac{r_4\gamma_4}{\mu_4\sigma_4}$, whereas the value of N_4 for the same fixed point is in the first quadrant if the exergy flow available to N_1 and N_4 is greater than a certain threshold, given by $\frac{\sigma_4\mu_4\gamma_4}{r_4\gamma_1} N_1^*$, proportional to the numerosity N_1^* of the species N_1, to the minimum specific exergy consumption rate of N_4, to the mortality rate and efficiency of N_4 to gain net exergy flows and inversely proportional to the birth rate of the species N_4 and to the efficiency of N_1 to gain net exergy flows. From the above analysis it follows that there is at least one fixed point, given by a), that is always present, and we can have up to 3 fixed points.

Let us look at the stability of the points in Table 1. The Lyapunov exponents, determined by the linearized system corresponding to (7a-7b), are listed in Table 2 for the fixed point a) and b).

Table 2: The Lyapunov exponents of the two fixed points a) and b) in Table 1.

	λ_1	λ_2
a)	$-\mu_1$	$-\frac{r_4\mu_4}{r_4+\mu_4}$
b)	$-\frac{\mu_1\sigma_1}{E_1(\mu_1+r)} N_1^*$	$\left(\frac{\gamma_4 r_4\dot{E}_1-\sigma_4\gamma_1\mu_4 N_1^*}{\gamma_4\dot{E}_1+\sigma_4\gamma_1 N_1^*}\right)$

Point a) is always stable, whereas the point b) is in the first quadrant only if $\dot{E}_1 > \frac{\mu_1 T}{r_1}$ and, in addition, is stable only if $\lambda_2 = \frac{\gamma_4 r_4\dot{E}_1-\sigma_4\gamma_1\mu_4 N_1^*}{\gamma_4\dot{E}_1+\sigma_4\gamma_1 N_1^*}$is negative. This is the case if $\frac{\gamma_1 r_1}{\mu_1\sigma_1} > \frac{\gamma_4 r_4}{\mu_4\sigma_4}$ and $\dot{E}_1 > \frac{\gamma_1\mu_1\mu_4\sigma_4 T}{\gamma_1 r_1\mu_4\sigma_4-\gamma_4 r_4\mu_1\sigma_1}$. Notice that if this last condition is verified then the relation $\dot{E}_1 > \frac{\mu_1 T}{r_1}$ is automatically satisfied since $\frac{\gamma_1\mu_1\mu_4\sigma_4 T}{\gamma_1 r_1\mu_4\sigma_4-\gamma_4 r_4\mu_1\sigma_1} = \frac{\mu_1 T}{r_1} + \frac{\gamma_4\mu_1^2 r_4\sigma_1 T}{r_1(\gamma_1 r_1\mu_4\sigma_4-\gamma_4 r_4\mu_1\sigma_1)}$. In conclusion, the point $(N_1, N_4) =$

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$\left(0,\frac{r_4\dot{E}_1}{\sigma_4\mu_4}\right)$ is always stable, whereas point $(N_1,N_4)=\left(\frac{r_1\dot{E}_1-\mu_1 T}{\sigma_1\mu_1},0\right)$ $(N_1,N_4)=\left(\frac{r_1\dot{E}_1-\mu_1 T}{\sigma_1\mu_1},0\right)$ is in the first quadrant if $\dot{E}_1>\frac{\mu_1 T}{r_1}$ and it is also stable if $\frac{\gamma_1 r_1}{\mu_1\sigma_1}>\frac{\gamma_4 r_4}{\mu_4\sigma_4}$ and $\dot{E}_1>\frac{\gamma_1\mu_1\mu_4\sigma_4 T}{\gamma_1 r_1\mu_4\sigma_4-\gamma_4 r_4\mu_1\sigma_1}$.
Let us now look at point c). From Table 1) it is clear that it falls in the first quadrant if $\frac{\gamma_1 r_1}{\mu_1\sigma_1}>\frac{\gamma_4 r_4}{\mu_4\sigma_4}$ and $\dot{E}_1>\frac{\gamma_1\mu_1\mu_4\sigma_4 T}{\gamma_1 r_1\mu_4\sigma_4-\gamma_4 r_4\mu_1\sigma_1}$. So, let us assume that these relations are satisfied. By linearizing the system of equations (7a-7b) around point c), we can write the quadratic equation for the Lyapunov exponents as:

$$\lambda^2+W\lambda-\frac{\mu_1 r_4[(\gamma_1 r_1\mu_4\sigma_4-\gamma_4 r_4\mu_1\sigma_1)\dot{E}_1-\gamma_1\mu_1\mu_4\sigma_4 T]}{\dot{E}_1\gamma_1\sigma_4(\mu_1+r_1)(\mu_4+r_4)}=0 \qquad (8)$$

where W is a complicated expression containing the parameters of the model. If point c) were stable, both roots of equation 4) would have a negative real part and this would be the case if all the coefficients of λ^k, $k=0,1,2$ had the same sign. But the signs of the coefficients of λ^2 and λ^0 are opposite, since we are assuming that $\dot{E}_1>\frac{\gamma_1\mu_1\mu_4\sigma_4 T}{\gamma_1 r_1\mu_4\sigma_4-\gamma_4 r_4\mu_1\sigma_1}$. It follows that point c) is unstable.
To better understand what happens in the phase space (N_1,N_4) we divide the semi-plane $\{N_1>0,N_4>0\}$ in different regions according to the sign of $\dot{N}_1$ and $\dot{N}_4$. So we define a line and a curve given by the following expressions:

$$N_4=\frac{r_4\dot{E}_1}{\mu_4\sigma_4}-\frac{\gamma_1 N_1}{\gamma_4} \qquad (9a)$$

$$N_4=\frac{N_1\gamma_1((r_1\dot{E}_1-\mu_1 T)-N_1\mu_1\sigma_1)}{\gamma_4\mu_1(\sigma_1 N_1+T)} \qquad (9b)$$

Eqtns. 9a) and 9b) can be represented on a N_1/N_4 plane (figures 3 and 4): in the region below the line 9a) $\dot{N}_4>0$ and in that below the line 9b) we have $\dot{N}_1>0$. Depending to the relative size of the parameters $\frac{\gamma_1 r_1}{\mu_1\sigma_1}$ and $\frac{\gamma_4 r_4}{\mu_4\sigma_4}$ and the relative size of $\dot{E}_1$ and T we can have the following scenarios:

i. $\dot{E}_1<\frac{\mu_1 T}{r_1}$. In this case there exists only the fixed point a) and species N_1 will reach extinction.
ii. $\frac{\mu_1 T}{r_1}<\dot{E}_1<\frac{\mu_1 T}{r_1}+\frac{\gamma_4\mu_1^2 r_4\sigma_1 T}{r_1(\gamma_1 r_1\mu_4\sigma_4-\gamma_4 r_4\mu_1\sigma_1)}$. In this case there are two fixed points: a) and b), the former being stable and the latter unstable. Again N_1 will reach extinction.
iii. $\dot{E}_1>\frac{\mu_1 T}{r_1}+\frac{\gamma_4\mu_1^2 r_4\sigma_1 T}{r_1(\gamma_1 r_1\mu_4\sigma_4-\gamma_4 r_4\mu_1\sigma_1)}$ and $\frac{\gamma_1 r_1}{\mu_1\sigma_1}<\frac{\gamma_4 r_4}{\mu_4\sigma_4}$. In this case there are two fixed points: a) and b), and a) is stable and b) unstable. Again N_1 will reach extinction.
iv. $\dot{E}_1>\frac{\mu_1 T}{r_1}+\frac{\gamma_4\mu_1^2 r_4\sigma_1 T}{r_1(\gamma_1 r_1\mu_4\sigma_4-\gamma_4 r_4\mu_1\sigma_1)}$ and $\frac{\gamma_1 r_1}{\mu_1\sigma_1}>\frac{\gamma_4 r_4}{\mu_4\sigma_4}$. In this case all three fixed point of Table 1) lie in the semi-plane $\{N_1>0,N_4>0\}$: a) and b) are stable whereas c) is unstable. Which one of the two species N_1 and N_4 will become extinct essentially depends on the initial conditions as explained below.

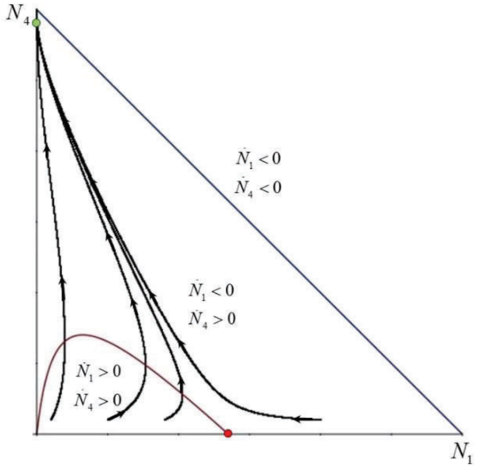

Figure 3: Line 9a) is in blue, 9b) in red, and the black lines describe the evolution of N_1 corresponding to different initial conditions. The green fixed point is stable, the red one is unstable.

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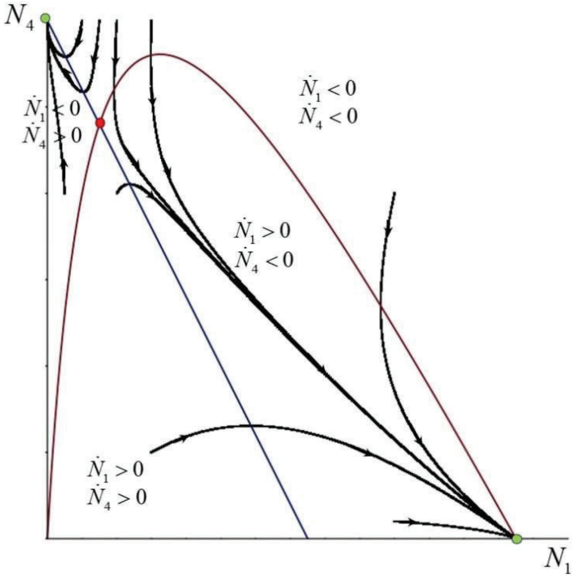

Figure 4: Line 9a) is in blue, 9b) in red, and the black lines describe the evolution of N_1 corresponding to different initial conditions. There are two stable fixed points (in green) and one unstable (in red).

Let us assume that we are in the case ii. described above. Line 9a) is above the curve 9b) and the two do not touch in the first quadrant. This type of scenario is depicted in Figure 3): under the curve 9b) both $\dot{N}_1$ and $\dot{N}_4$ are positive, i.e. N_1 and N_4 are increasing in time. Between the two curves N_1 decreases and N_4 increases. In the region above line 9a) both populations decrease.

For scenario iv, the two curves intersect and the semi-plane $\{N_1 > 0, N_4 > 0\}$ is divided into four regions, each having a different combination of the sign of the derivatives of N_1 and N_4 (Figure 4). In the region above the curve 9a) and 9b) both numerosities decrease. Above 9b) and below 9a) N_1 decreases and N_4 increases. Below 9b) and above 9a) N_1 increases and N_4 decreases, and finally in the region above both curves the two numerosities increase.

3.2 Application of the model to real data

In this section we briefly discuss the evolution of the numerosities by introducing real (i.e., empirically available) values for the model parameters. Apart birth and death rates and minimum consumption for survival, given by the terms σ_i, a crucial role is played by the exergy flow inputs $\dot{E}_1$ and the term that we labelled as "competition exergy" $T = \chi_{12}N_2 + \chi_{13}N_3$. It is difficult to accurately estimate the latter because the competition factors χ_{12} and χ_{13} depend on different and not always deterministic boundary conditions; besides, their average could be also fluctuating in time. For these reasons we prefer to consider T as a parameter. The exergy flow available to the species, $\dot{E}_1$, can be estimated in different ways: without further justifications, let us assume it is a fraction of the incoming solar irradiation, whose average value for that region of New Zealand is 1400 kWh/(m^2 yr). As for the other parameters, the values reported in Table 3 represent our best estimates, which are the "base-case" parameters. These values have been extrapolated from the literature: for the intrinsic growth rate and the maximum mortality rate of the Kakapos we made an estimation from the data given by the Department of Conservation Te Papa Atawhai of New Zealand (2022). For the specific exergy consumption rates corresponding to a minimum survival of the corresponding species we took the values from Harris et al. (1985) for the possums and from Bryant (2006) for the Kakapos. For the relative ratio of the $\gamma's$ we look at Atkinson & Merton (2006).

In Figure 5 we report the numerical solutions starting from different initial conditions: $N_1(0) = 200$, $N_1(0) = 520$, $N_1(0) = 530$ and $N_1(0) = 1200$. The values of $N_4(0)$ have all been taken to be equal to 1000. Since there are two stable fixed point, the plane (N_1, N_4) is divided into a region in which the solution will be attracted to the stable point a) (the "basin of attraction of point a") and another in which it will evolve towards the stable point b) (the basin of attraction for point b"): the shapes of these regions

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are extremely sensitive to the values of the model parameters. It is also clear from Figure 5 that the global behavior of the solution (i.e. to which point the solution is attracted) is very sensitive to the initial conditions: a small change therein will change the basin of attraction into which the solution will end up.

Considering that the total area of the Codfish, Little Barrier and Maud Island is of about 58.5 km^2, we find a limit specific carrying capacity of about 2800 Kakapos/km^2. Clearly this number is an exergetic limit, the real number can be a fraction lower than this for many reasons: not all the territory of the island is accessible to the Kakapos, the real feeding area is further reduced due to the impossibility to reach the vegetation in steeper or inaccessible regions. Further the Kakapos are known to have a solitary behavior, indeed adult males and females meet only to breed, and also this aspect reduces the available territory, currently evaluated to be about 1000 meters square for each male (notice that indeed 2800 Kakapos/km^2 are 2.8 in each 1000 meters square). The previous aspects, and in particular those related to the personality of this species, have been necessarily left out in this work. In general, if $\dot{E}_1 > \frac{\mu_1 T}{r_1} + \frac{\gamma_4 \mu_1^2 r_4 \sigma_1 T}{r_1(\gamma_1 r_1 \mu_4 \sigma_4 - \gamma_4 r_4 \mu_1 \sigma_1)}$ and $\frac{\gamma_1 r_1}{\mu_1 \sigma_1} > \frac{\gamma_4 r_4}{\mu_4 \sigma_4}$, for given parameters there will be a threshold value N_1^* such that if $N_1(0) > N_1^*$ the Kakapos will be out of the extinction risk. In real life the parameters are not constant in time and the basins of attraction may change their shape in time. The threshold value N_1^* also will depend on time and thus it would be more accurate to state that $N_1(0) > \sup_{t>0} N_1^*(t)$.

Table 3: The semi-empirical model parameters assumed in the simulation.

$\dot{E}_1$	Net exergy resource input into the niche	16	kW/km^2
T	Competition parameter as per eqtn. (7-a,b)	1	kW/km^2
r_1	Intrinsic growth rate of species 1	0.22	years^{-1}
r_4	Intrinsic growth rate of species 4	2	years^{-1}
μ_1	Intrinsic mortality rate of species 1	0.18	years^{-1}
μ_4	Intrinsic mortality rate of species 4	1.5	years^{-1}
σ_1	Minimum survival exergy consumption of species 1	6.6 10^{-3}	kW/individual
σ_4	Minimum survival exergy consumption of species 4	4.5 10^{-3}	kW/individual

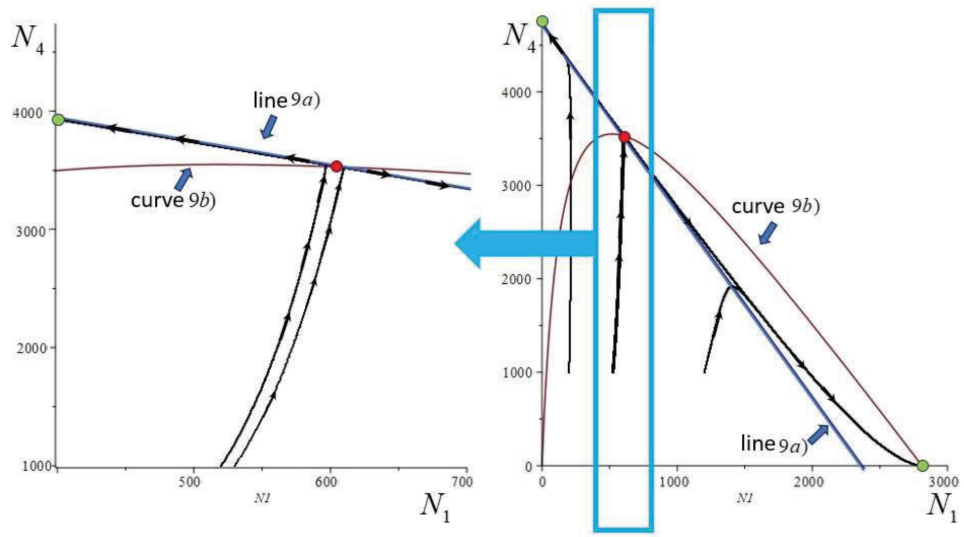

Figure 5: Line 9a) is in blue, 9b) in red, and the black lines describe the evolution of N$_1$ and N$_4$ corresponding to different initial conditions.

Legenda: The figure on the right is the representation of the behaviour of the system in the plane (N_1, N_4) (this may be seen as an instantiation of figures 3 and 4 using empirical values for the model

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parameters). To the left a magnification of the zone ($400< N_1 < 600$): the flows corresponding to two rather close initial conditions $N_1(t=0)=520$ and $N_1(t=0)=530$ end up in different attraction points. Here $\gamma_1 = 2\gamma_4$, the other parameters as in Table 3.

Summarizing: if either one of the conditions $\dot{E}_1 > \frac{\mu_1 T}{r_1} + \frac{\gamma_4 \mu_1^2 r_4 \sigma_1 T}{r_1(\gamma_1 r_1 \mu_4 \sigma_4 - \gamma_4 r_4 \mu_1 \sigma_1)}$ and $\frac{\gamma_1 r_1}{\mu_1 \sigma_1} > \frac{\gamma_4 r_4}{\mu_4 \sigma_4}$ is not satisfied the Kakapos will get extinct for any set of initial conditions. The previous equation can be read in different ways: for example the relation $\dot{E}_1 > \frac{\mu_1 T}{r_1} + \frac{\gamma_4 \mu_1^2 r_4 \sigma_1 T}{r_1(\gamma_1 r_1 \mu_4 \sigma_4 - \gamma_4 r_4 \mu_1 \sigma_1)}$, for any fixed set of parameters $(\gamma_1, \gamma_4, r_1, r_4, \mu_1, \mu_4, \sigma_1, \sigma_4)$, cannot be satisfied if the value of the competition exergy $T = \chi_{12} N_2 + \chi_{13} N_3$ is larger than a given threshold value then surely the Kakapos will get extinct. Notice that this value increases by increasing the exergy inflow rate $\dot{E}_1$. The relation $\frac{\gamma_1 r_1}{\mu_1 \sigma_1} > \frac{\gamma_4 r_4}{\mu_4 \sigma_4}$ is also crucial: it can be read as: the efficiency of the Kakapos to gain net exergy flows is greater then the efficiency of their main food competitors. There are different ways to increase this efficiency: it is possible to increase the value of the constant γ_1 by inserting supplementary feeding closer to the Kakapos habitat, it is possible to increase the value of r_1 by recurring to artificial insemination techniques. If both the previous relations are not satisfied, still there is the possibility for the Kakapos to get extinct if the numerosities of the two species fall in given regions of the plane $(N_1\ N_4)$.

4 CONCLUSIONS

Following a line of work that tries to establish a semi-deterministic correlation between the available resources in a certain niche, the metabolic and feeding characteristics of the species inhabiting the niche and the modes of interaction among these species, we present here an assessment of the situation of a strongly endangered species, the New Zealand Kakapo. A model is constructed in which the species under study (N_1, the Kakapo) has a direct competitor for resources (N_4, the Possum), and is preyed upon by two predators (N_2, the Rat, and N_3, the Stout). The top predator in the niche is the Stout, who preys also on rats. While the Kakapo is endemic to New Zealand, the other three species were introduced in relatively recent times by humans: as a result, the Kakapo's defensive strategy resulting from a long-time adaptation to its endemic predators (eagles and harriers) does not work against the alien species. Even under the limitations of strongly approximated values for the model parameters and of the uncertainty about the actual numbers of predators, the model predicts a very dire end for the Kakapo, unless strong conservationist measures are taken, consisting in the complete elimination of their alien competitors. The most recent efforts of the New Zealand authorities seem to go in this direction, but if our model is accurate in its predicting the very frail equilibrium of the Kakapos survival in their niche, a constant and long-range effort will be required to bring back the numerosity of the species to anything resembling the values it attained before the human colonization of the region.

NOMENCLATURE

N	Population numerosity	
E	Exergy flow rate	(W)
T	Competition exergy flow rate	(W)
n	Birth rates	(years^{-1})
m	Death rates	(years^{-1})
r	Limit growth rate	(years^{-1})
β_i	Fraction of the exergy flow rate at the species i	(W)
γ_i	Inflow capture coefficient	(W/individual)
μ_i	Intrinsic mortality rate	(years^{-1})
σ_i	Minimum consumption for survival of I	(W/individual)
χ_{ij}	Competition coefficient between N_i and N_j	(W/individual)

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