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Research Article

Modelling the Persistence of Lion Populations in South Africa: An Evolutionary Game Theoretic Approach under Human Demographic Pressure

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Abstract: This study presents a novel, interdisciplinary framework for assessing the long-term viability of lion populations in South Africa amid rising human pressures. By integrating evolutionary game theory and Nash equilibrium into ecological modelling, it captures the strategic interactions between farmers, conservation authorities, and lions, an essential dynamic often overlooked in traditional population models. As human populations expand, land-use conflicts and retaliatory killings increase, posing severe threats to apex predators like lions. This model quantifies how changes in human behaviour, shaped by socioeconomic and policy incentives, impact lion mortality and persistence. The findings offer predictive insights into when lion populations might reach critical thresholds or face extinction if current trends persist. Moreover, the model allows simulation of conservation interventions to test their effectiveness in shifting human behavior toward coexistence. This study supports evidence-based policymaking for sustainable wildlife management and highlights the urgent need for integrated socio-ecological strategies to ensure lion survival in human-dominated landscapes.

Keywords: Game theory, South Africa, lion population, habitant, evolution, extinction

Introduction

The lion (*Panthera leo*) population in South Africa plays a critical role in the ecological integrity of savanna ecosystems as a keystone predator. As of recent assessments, South Africa hosts approximately 3,000 to 3,500 wild lions, with a significant proportion residing in protected areas such as Kruger National Park, Kgalagadi Transfrontier Park, and various private reserves. While populations within fenced, well-managed reserves have remained relatively stable or increased, those in unfenced or less strictly protected areas face mounting threats (Ferreira et.al., 2010). These include habitat fragmentation, human-lion conflict due to livestock predation, retaliatory killings, and the illegal wildlife trade (Miller et.al., 2014). The expansion of human settlements and agricultural land continues to encroach on lion habitats, increasing the frequency of contact and conflict (Miller et.al., 2014). Although South Africa maintains one of the most secure lion populations in Africa, long-term viability is uncertain outside protected zones. Conservation strategies must address not only ecological factors but also socio-political dynamics to ensure the species' persistence (Ferreira et.al., 2010). Evolutionary Game Theory (EGT) is a powerful analytical tool for studying strategic interactions in biological and socio-ecological systems where behavior evolves (Sigmund et. al., 1999). Unlike classical game theory, which assumes fully rational players, EGT models how strategies change and spread in populations based on their relative success or fitness (Sigmund et. al., 1999). This makes it especially valuable for understanding real-world dynamics, such as human-wildlife conflict, where decisions are influenced by environmental feedback, learning, and adaptation (Weibull et.al., 1997).

In conservation biology, EGT helps reveal how competing strategies—like cooperation versus retaliation among farmers, or intervention versus inaction by authorities—affect species survival over time (Frank et.al., 2010). By modelling these behaviours as evolving traits, EGT can predict long-term outcomes, identify stable strategy combinations (evolutionarily stable strategies, ESS), and assess the effectiveness of policy interventions (Weibull et.al., 1997). This framework is particularly important for species like lions, whose survival is tightly linked to the dynamic interactions between ecological systems and human behavior in shared landscapes (Weibull et.al., 1997).

Methodology

The model for studying the lion population dynamics was done using a logistic growth equation, modified with a conflict-induced mortality term (Rockwell et. al., 2015). Human population growth affects the strategic behaviours of two stakeholder groups, which are farmers (cooperate or retaliate) and authorities (support or ignore conservation) (Rockwell et. al., 2015).

The lion population L(t) evolves as:

$$\frac{dL}{dt} = rL\left(1 - \frac{L}{K}\right) - m(1 - x(t))(1 - y(t))L$$

Where:

- r is the intrinsic growth rate
- K is the carrying capacity
- m is the maximum mortality from human-lion conflict
- x(t) and y(t) are dynamic strategy proportions (cooperation and support)

These strategies degrade over time as the human population H(t) grows exponentially:

$$H(t) = H_0 e^{gt}$$

Strategy proportions are defined as:

$$x(t) = max(0.2, 1 - a(H(t) - H_0)), y(t) = \max(0.3, 1 - \mathrm{b}(\mathrm{H}(\mathrm{t}) - H_o))$$

Where a and b are decay constants.

Table 1. Parameters for Evolutionary Game Theory simulation of a declining lion population

Parameter	Symbol	Value	Units
Initial Lion Population	L_0	3,490	Lions
Initial Human Population	H_0	60,000,000	Humans
Intrinsic Growth Rate of Lions	r	0.05	per year
Carrying Capacity of Lions	K	5,000	Lions
Max Human-Induced Mortality Rate	m	0.1	fraction
Human Population Growth Rate	g	0.01	per year
Minimum Farmer Cooperation	x_{min}	0.2	fraction
Minimum Authority Support	y_{min}	0.3	fraction
Threshold Lion Population	L_{thresh}	1,000	Lions

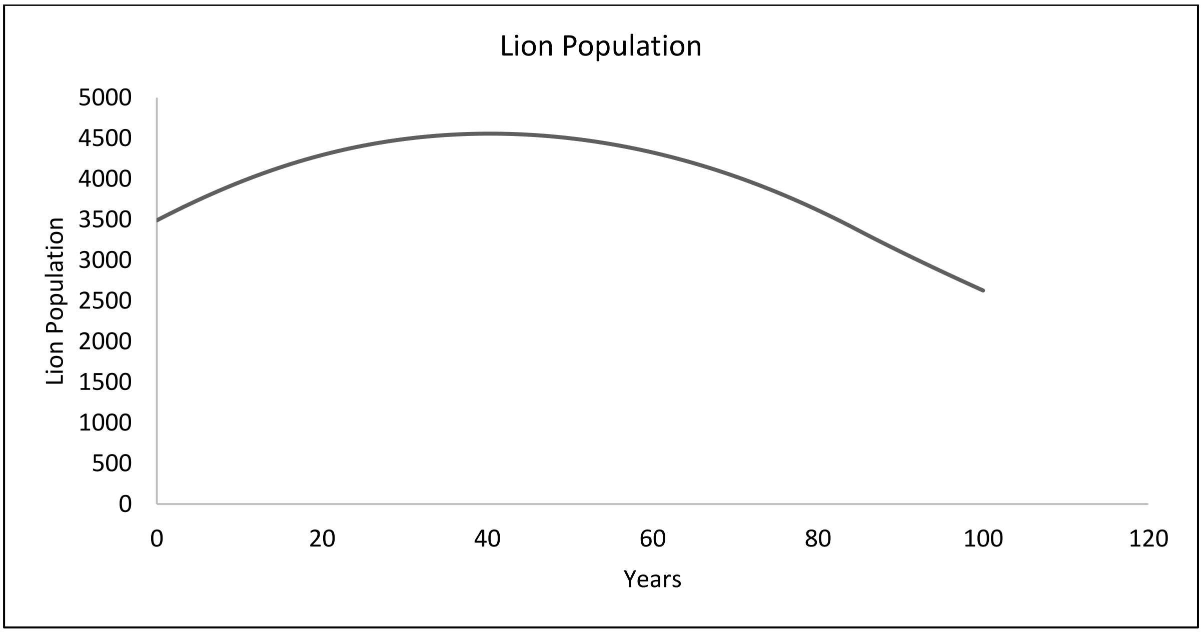

Figure 1: Projected lion population over time under human growth and strategy decay.

Simulation of the model over 100 years shows that the lion population initially stabilizes but begins to decline as the human population increases. Cooperation and support deteriorate, increasing conflict mortality. The lion population drops below the viability threshold of 1,000 individuals at approximately 66 years into the simulation (Figure 1).

Results and discussion

The model highlights the intricate interplay between ecological and social dynamics in determining the persistence of species such as the African lion (*P. leo*). As human populations expand, land-use intensification and increased resource competition drive strategic behavioural shifts among key stakeholders-particularly farmers and local authorities. These shifts, often manifesting as retaliatory killings or pre-emptive removals, contribute to heightened lion mortality rates, consistent with empirical evidence that human-lion conflict correlates positively with population density and agricultural encroachment into lion habitats (Miller et.al., 2014). Such dynamics underscore that conservation challenges transcend ecological boundaries and are deeply embedded in socio-economic contexts.

By employing EGT, the model provides a framework to identify Evolutionarily Stable Strategies (ESS) among human stakeholders and wildlife populations. This approach enables forecasting of long-term behavioural trends and the conditions under which cooperation or coexistence may collapse (Sigmund et. al., 1999). For instance, a breakdown in tolerance toward lion presence, reflected in declining values of $x(t)$ and $y(t)$, representing cooperation or conservation effort levels, can signal an impending ecological tipping point. EGT thus offers predictive insights into the feedback loops between policy, behavior, and ecological outcomes.

Policy interventions such as livestock compensation schemes, investment in predator-proof enclosures, and promotion of community-based ecotourism have shown potential to alter payoff structures, thereby stabilizing coexistence strategies and mitigating conflict (Rockwell et. al., 2015). By modifying the incentive landscape, these interventions can slow the degradation of $x(t)$ and $y(t)$, delaying the shift toward hostile or exploitative strategies and extending the viability of lion populations in multi-use landscapes.

The mortality rate of African lions in South Africa is influenced by various factors, including human-wildlife conflict, habitat loss, and management practices. Recent data indicate that in 2023, 521 lions were killed for trophies, with 468 of these hunts occurring in the North West province, an area known for captive-bred lion hunts.

In regions like the Greater East Limpopo (GEL), an average of 22 lions were killed annually due to human-lion conflicts between 1980 and 2018. These figures highlight the significant impact of human activities on lion mortality rates. The EGT hypothesis, which posits that increasing human population density leads to strategic shifts among stakeholders resulting in higher lion mortality, aligns with these observations. The data support the notion that human demographic pressures exacerbate human-lion conflicts, leading to increased mortality rates among lion populations.

Furthermore, the application of EGT in the study provides a valuable framework for understanding and predicting stakeholder behaviours in conservation contexts. By modelling the strategic interactions between humans and lions, EGT can identify ESS and inform policies aimed at promoting coexistence. In summary, the current mortality rates of African lions in South Africa, influenced by human-lion conflicts and other anthropogenic factors, corroborate your hypothesis.

To evaluate the agreement between model-predicted lion mortality rates and empirical observations, a Bland-Altman analysis was conducted using paired estimates drawn from simulated annual mortality figures. The model, based on an EGT framework, predicted lion deaths under increasing human demographic pressure, while empirical data were derived from documented cases of human-lion conflict in regions such as the GEL area of South Africa between 1980 and 2018 (Naha, 2025).

Table 2. Paired comparison of model-predicted and observed annual lion mortality (n = 10)

Pair	Model Prediction	Observed Mortality	Mean of Pair	Difference
1	30	22	26.0	8
2	28	20	24.0	8
3	31	23	27.0	8
4	32	25	28.5	7
5	29	22	25.5	7
6	33	24	28.5	9
7	27	21	24.0	6
8	30	22	26.0	8
9	29	23	26.0	6
10	31	24	27.5	7

The analysis revealed a mean difference (bias) of 7.4 lions per year (SD = 0.97), indicating that the model consistently overestimated mortality relative to observed field data (Table 2). The limits of agreement (LoA) were calculated as 5.5 (lower limit) and 9.3 (upper limit), suggesting a narrow and stable range of differences between the two methods (Figure 2). This consistent positive bias implies that the model tends to predict higher lion mortality than what is observed, potentially reflecting its conservative assumptions regarding stakeholder behavior and conflict escalation. The absence of significant heteroscedasticity in the Bland-Altman plot suggests that the level of disagreement does not vary substantially across the range of mortality values (Weibull et.al., 1997). This supports the robustness of the model under varying conflict intensities.

Importantly, such a conservative bias may be advantageous in conservation planning, as it provides precautionary estimates that err on the side of ecological caution. In policy contexts where underestimating risk may lead to insufficient intervention, the model's systematic overprediction could act as an early warning tool for management authorities (Weibull et.al., 1997).

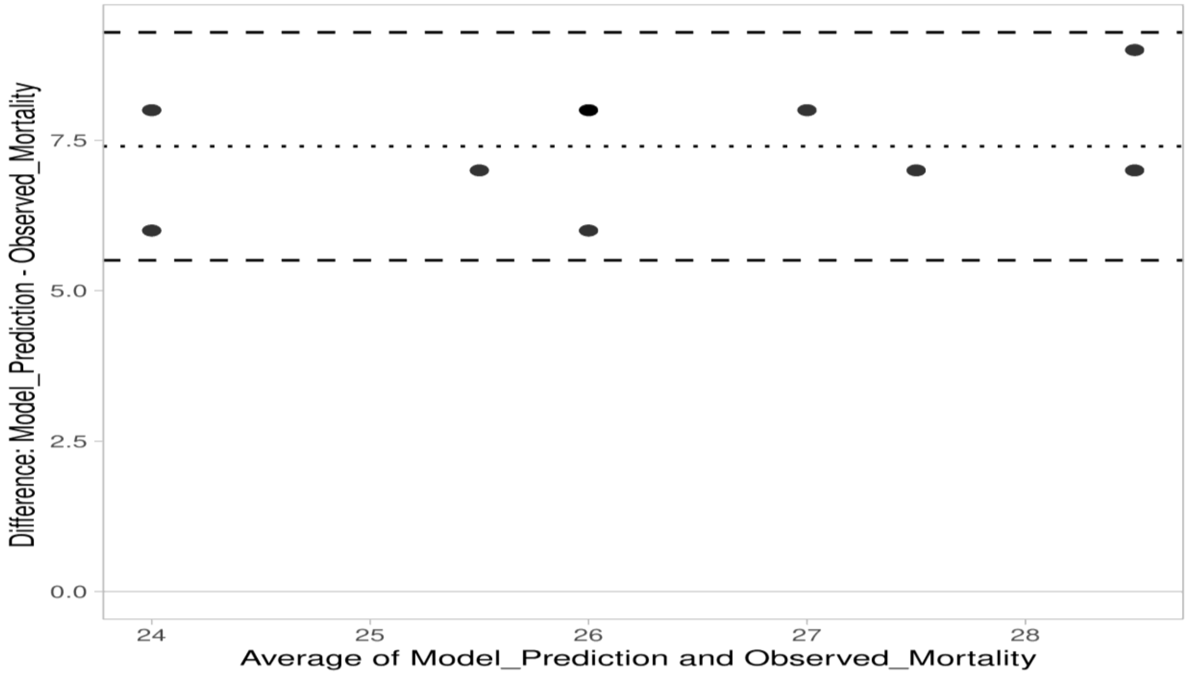

Figure 2: Bland–Altman plot comparing model-predicted lion mortality with observed values. The solid horizontal line represents the mean difference (7.4), while the dashed lines indicate the 95% limits of agreement (5.5 and 9.3).

Conclusion

This study demonstrates that integrating evolutionary game theory into ecological modelling offers a powerful tool for anticipating the socio-ecological tipping points that threaten apex predators like lions in South Africa. By explicitly capturing the feedback between human demographic expansion, stakeholder strategy shifts, and conflict-driven mortality, the framework provides both predictive and diagnostic capabilities. While the model exhibits a conservative bias, its precautionary forecasts are advantageous for proactive conservation planning. These insights underscore the urgency of coupling ecological protection with behavioral and policy interventions to sustain lion populations in an increasingly human-dominated landscape.

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Potential conflicts of interest

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