Niche construction by cooperative hunting and reproductive skew

Project Summary

Overview

Different types of cooperative behaviors may select for each other, and cooperative behaviors can have dramatic effects on their ecological communities.

Despite the prominence of cooperatively hunting species in conservation efforts, and their recognition in structuring communities, the ecology of their cooperative hunting behavior is not well understood.

The PI's focus on cooperative hunting primarily, and also on whether it may select for or against reproductive skew

The PI will answer the following questions: (1) Can availability of profitable big prey, combined with competition for less profitable small prey, drive the formation of groups of predators? (2) If predators form groups, do they then drive the prey to extinction, (3) Does reproductive skew limit or encourage the evolution of cooperative hunting?

Intellectual Merit

Evolution of social behavior and ecology some social behavior incorporated into predator-prey models, primarily in prey, but not in predators in a way that reflects the trade-offs of cooperation, i.e., weighing the benefit of accessing new types of prey versus having to share what is caught.

Additionally, exploring how different cooperative behaviors reciprocally create a niche.

Broader Impacts

Project Description

Introduction

Studying the ecological context of cooperative behaviors may elucidate why extreme examples of cooperation evolved. Two particularly interesting types of cooperative behavior are cooperative hunting and reproductive skew

   Studying social behavior in ecology is hard because there is very scant modeling of sociality in predator-prey dynamics, particularly with sociality of predators, and limited options for modeling the evolution of any behavior in a populaiton that is structured into groups.

   The P.I. proposes to conduct three projects:

1. The interaction of group formation dynamics and population dynamics

2. The evolution of reproductive skew with a population structured into groups that can hunt cooperatively or solitarily.

3. meta-analysis of cooperative hunting behavior, group dynamics, and reproductive cooperation across carnivora

Project 1: Predator Group Formation And Prey Dynamics

The predator population, with population size p, hunts two types of prey: big prey, with population size M_1, and small prey, with population size M_2. Big prey and small prey are also referred to as prey types 1 and 2, respectively. Predators are split into hunting groups that are of size $x \in 1, 2, \cdots, p$. Let $f(x, t)$ be the number of groups of size x, which for brefity is also written as $f(x)$. The population dynamics of predators and prey are

$$\frac{dp}{dt} = \sum_{x=1}^{x_m} f(x) \left[b_1 Y_1(x, M_1, M_2) + b_2 Y_2(x, M_1, M_2) \right] - p\delta \tag{1a}$$

$$\frac{dM_1}{dt} = g_1 M_1 \left(1 - \frac{M_1}{k_1} \right) - \sum_{x=1}^{x_m} f(x) Y_1(x, M_1, M_2) \tag{1b}$$

$$\frac{dM_2}{dt} = g_1 M_1 \left(1 - \frac{M_1}{k_1} \right) - \sum_{x=1}^{x_m} f(x) Y_2(x, M_1, M_2) \tag{1c}$$

where the parameters are defined in Table 1 and $Y_i(x, M_1, M_2)$ is the functional response on prey i. The functional responses are defined as the rate of prey caught per hunting *entity*, i.e. a solitary predator or predator group, so the fitness from hunting in a group is shared across the group WHICH IS NOT PRESENT IN OTHER PRED-PREY MODELS WITH COOPERATIVE HUNTING. The functional response of a hunting group of size x is a type II functional response (CITE HAMILTON?), namely

$$Y_i(M_1, M_2, x) = \frac{a_i \alpha_i(x) M_i}{1 + \sum_{j=1,2} a_j \alpha_j(x) h_j M_j}, \qquad \alpha_i(x) = \frac{1}{1 + e^{-\theta_i(x - s_i)}} \tag{2}$$

28   for $i = 1, 2$. The parameters are defined in Table 1. Importantly, the predator group size influences
29   the capture probability $\alpha_i(x)$, which is the probability a predator captures prey i upon encounter
30   (Fig. 1B). However, the combination of parameter θ_i, s_i are not very intuitive for understanding
31   how the capture probability responds to group size, especially since increasing θ_i, s_i also changes
32   the capture probability of solitary predators. For $\alpha_i(1)$ the capture probability of prey i by solitary

33   predators, $\theta_i = -\frac{\ln\left(\frac{1}{\alpha_i(1)} - 1\right)}{1 - s_i}$ is substituted into eq. 2.

34   Predator life cycles proceed as follows: Predators are born, go through a juvenile stage in
35   which they do not hunt (and are instead fed by the hunting parent), and then disperse, becoming
36   solitary until they join a group (if they join a group). Juveniles do not count toward group size
37   because they do not hunt, and the food they receive is provided by the share of food given to
38   the parent producing them. Predators may leave and join groups multiple times within their
39   lifespan. The time constant for group dynamics is τ_x. While time for the population dynamics
40   processes in system eqs. 1 is on the order of years or seasons, time for group dynamics may be
41   on the order of days, so $\tau_x \ll 1$. Thus the group size distribution changes from the following
42   processes: (1) solitary individuals join group of size x at rate $\psi(x)$, (2) individuals leave groups
43   of size x at rate $\phi(x)$, (3) Individuals die at rate $\delta\tau_x$, the death rate relative to the time scale of
44   group dynamics, and (4) individuals are born and disperse, becoming solitary, at a rate that is
45   the overall birth rate of predators, adjusted for the group formation time scale, i.e. $\tau_x \sum_{x=1}^{x_m} f(x)x\bar{w}$
46   , where $\bar{w}$ is defined in eq. 6. The master equations for the number of solitary individuals is, the
47   number of groups of size 2, and number of groups of size $x \geq 2$ are, respectively,

$$\tau_x \frac{\partial f(1)}{\partial t} = \underbrace{\tau_x \sum_{x=1}^{x_m} f(x)x\bar{w}(x)}_{\text{births}} + \underbrace{2 \cdot f(2)\phi(2)}_{\substack{\text{groups of 2} \\ \text{split to two solitaries}}} + \underbrace{\sum_{x=3}^{x_m} f(x)\phi(x)}_{\substack{\text{individuals leave} \\ \text{larger groups}}} + \underbrace{2f(2)\delta\tau_x}_{\substack{\text{larger groups shrink} \\ \text{due to deaths}}}$$

$$- \underbrace{f(1)\delta\tau_x}_{\substack{\text{deaths of} \\ \text{solitaries}}} - \underbrace{f(1)\sum_{x=2}^{x_m} \psi(x-1)}_{\substack{\text{solitaries join} \\ \text{groups}}}, \quad (3)$$

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$$\tau_x \frac{\partial f(2)}{\partial t} = - \underbrace{f(2)\phi(2)}_{\substack{\text{an individual} \\ \text{leaves}}} - \underbrace{f(2)\psi(2)}_{\substack{\text{growing to} \\ \text{larger group}}} + \frac{1}{2}\underbrace{f(1)\psi(1)}_{\substack{\text{solitaries} \\ \text{forming dyads}}} + \underbrace{f(3)\phi(3)}_{\substack{\text{a member leaves} \\ \text{a larger group}}} -2f(2)\delta\tau_x + 3f(3)\delta\tau_x \quad (4)$$

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$$\tau_x \frac{\partial f(x)}{\partial t} = - \underbrace{f(x)\phi(x)}_{\substack{\text{an individual} \\ \text{leaves}}} - \underbrace{f(x)\psi(x)}_{\substack{\text{growing to} \\ \text{larger group}}} + \underbrace{f(x-1)\psi(x-1)}_{\substack{\text{smaller group} \\ \text{grows to size } x}} + \underbrace{f(x+1)\phi(x+1)}_{\substack{\text{a member leaves} \\ \text{a larger group}}} - xf(x)\delta\tau_x, \quad (5)$$

50   where $\bar{w}(x)$ is the per-capita fitness in a group of size x if food is shared evenly, namely

$$\bar{w}(x) = \frac{1}{x}\left(b_1 Y_1(x, M_1, M_2) + b_2 Y_2(x, M_1, M_2)\right). \quad (6)$$

51   Let $S(x, y)$ be the best response function modeling the probability a decision-maker will tran-
52   sition from a group of size y to a group of size x, for $x, y \geq 1$, $y \leq x_m$, and $x \leq x_m - 1$. If

predators can freely leave and join groups, then that decision-maker is the predator that is deciding whether to leave or join a group. If groups decide whether to admit or eject members, the decision-maker could be either any subordinate individual in a group or the dominant individual. This function is sigmoidal in shape, growing closer to 1 as $W(x) - W(y)$ increases. We model this choice using Tullock's contest success function [3], i.e.,

$$S(x,y) = \frac{W(x)^d}{W(x)^d + W(y)^d} \tag{7}$$

for d a positive scaling constant that determines the shape of $S(x,y)$. If individuals can freely join or leave groups, the rate at which individuals join a group of size x is

$$\psi(x) = \begin{cases} [f(1) - 1]\, S(2,1) & \text{if } x = 1 \text{ and } f(x) \geq 1 \\ f(1)S(x+1,1) & \text{if } 1 < x \leq x_m - 1 \\ 0 & \text{otherwise,} \end{cases} \tag{8}$$

If $F(1) < 1$, what should I do???? Should it just be $F(1)^2$? and the rate at which they leave a group of size x will be $\phi(x) = xS(1,x)$ for $x \leq x_m$.

Plan For Analysis And Preliminary Results

The P.I.'s intend to compare the model described in eqs. 1a - c and eqs. 3 - 5 to a model in which all predators are in groups of size x^*, described by eqs. 1a - c with $f(x) = p/x$ for $x = x^*$ and 0 otherwise. Initial results indicate that whereas froup group sizes to stay at a constant x^* can lead to one prey type going extinct, allowing fission-fusion dynamics of group sizes results in both prey types and predators coexisting. The P.I.'s will test whether increased availability selects for more cooperation by examining whether increasing growth rates of big prey increases average group size of predators. Furthermore, they will examine the range of parameters for which extinction of either prey type is locally stable using linear stability analysis. Finally, the authors will examine the presence or absence of apparent competition, as defined in [1], between prey types, and how apparent competition depends on group dynamics.

Project 2: The Evolution Of Reproductive Skew Across Dynamic Groups

DO I NEED THE SMALL PREY VS BIG PREY HERE, OR IS IT ENOUGH TO JUST SAY THEY GET A BIG YIELD IN A GROUP BUT IT HAS TO BE SHARED, THEY GET A SMALL YIELD ALONE BUT IT'S ALL THEIRS.

Predators can hunt large prey, which has benefit b_1 before sharing, or hunt small prey which has benefit b_2 before sharing. There are no population dynamics of big prey and small prey. Then the rate at which predator groups catch prey is similar to eq. 2 but the P.I.'s set $M_1, M_2 = 1$, so here

$$Y_i(x) = \frac{a_i \alpha_i(x)}{1 + h_1 a_1 \alpha_1(x) + h_2 a_2 \alpha_2(x)} \qquad \text{for } \alpha_i(x) = \frac{1}{1 + e^{-\theta_i(x - s_i)}}. \tag{9}$$

There are overlapping generations, so births increase relatedness, and the P.I.'s track relatedness for each group size? This might be similar to [2]. WE NEED TO DISCUSS HOW TO DO THIS?

Table 1: List of parameters used in the model

Parameter	Definition
b_1	Conversion of big prey caught to predator population growth; $0 < b_1 < 1$
b_2	Conversion of small prey caught to predator population growth; $0 < b_2 < B$
δ	Death rate of predators, i.e. the probability a predator dies per unit ecological time; $0 < \delta < 1$.
τ_x	The time constant for the dynamics of group size
θ_1	Facilitation by cooperation of predators hunting big prey; $\theta_1 \geq 0$
θ_2	Facilitation by cooperation of predators hunting small prey; $\theta_2 \leq 0$
h_1	Handling time of big prey
h_2	Handling time of small prey
a_1	Attack rate on big prey by solitary predator
a_2	Attack rate on small prey by solitary predator
γ	Portion of even share of food donated by subordinates

If this model does not track population dynamics then how do new individuals fit into the system? Are births balanced by deaths? So if $\sum_x f(x)\bar{w}(x)$ is the overall birth rate of the population, then the per-capita death rate is $\delta = \frac{1}{p}\sum_x f(x)\bar{w}(x)$ for $p = \sum_x x f(x)$ the constant population size.

Reproductive skew results in division of labor between a minority that devotes its time to reproducing, and a majority that devotes its time to hunting. Say predators spend a portion of their time t_h foraging, leaving a portion $1 - t_h$ of their time to reproduce. If there is reproductive skew, dominants spend all of their time reproducing, and skew increases as the portion of time spent hunting of subordinates t_h increases. The expected hunting group size for groups of size $x > 1$ is $\bar{x}_e(x) = t_h(x-1)$. Furthermore, reproduction of each individual is proportional to the yield after sharing and the time available to reproduce. So the reproduction of a subordinate is $w_s(x) = \frac{1}{x}(1 - t_h)\sum_{i=1,2} Y_i(\bar{x}_e(x))$ and that of a dominant is $w_d \frac{1}{x}\sum_{i=1,2} Y_i(\bar{x}_e(x))$. SO ISSUE HERE IS FOOD STILL SHARED EVENLY. COULD POSSIBLY SAY THE FOOD SUBORDINATES AREN'T SPENDING ON REPRODUCTION IS GOING TO THE DOMINANT?

Project 3: The Presence Of Cooperative Hunting, Cooperative Breeding, And Group Formation Across Carnivora

Broader Impacts

Results From Prior NSF Support
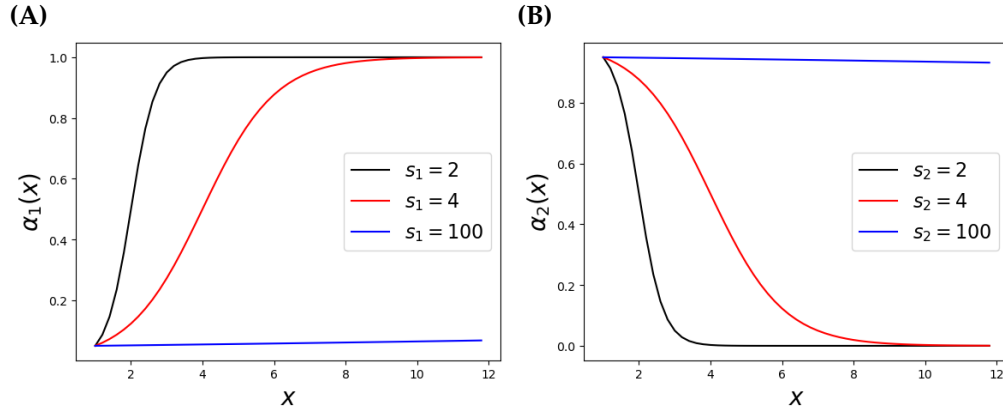

Figures

(A)

(B)

Figure 1: Capture probabilities of **(A)** big prey and **(B)** small prey where the capture probability for solitary predators if $\alpha_1(1) = 0.05$ for big prey and $\alpha_2(1) = 0.95$ for small prey. In panel **(A)**, the capture probability is shown for critical group sizes $s_1 = 2$ (black line), $s_1 = 4$ (red line), and $s_1 = 100$ (blue line). Similarly in panel **(B)**, the capture probability is shown for critical group sizes $s_2 = 2$ (black line), $s_2 = 4$ (red line), and $s_2 = 100$ (blue line)

References Cited

[1] Robert D. Holt. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, 12(2):197–229, October 1977.

[2] Rufus A. Johnstone. KIN SELECTION, LOCAL COMPETITION, AND REPRODUCTIVE SKEW. *Evolution*, 62(10):2592–2599, October 2008.

[3] Tullock, G. Efficient rent seeking. In Buchanan, J. M., Tollison, R. D., and Tullock, G., editors, *Toward a theory of the rent-seeking society*, pages 97–112. Texas A&M University Press, College Station, 1980.