

Niche construction by cooperative hunting and reproductive skew

Project Summary

Overview

- Different types of cooperative behaviors may select for each other, and cooperative behaviors may play a large role in structuring their ecological communities.
- Despite the prominence of cooperatively hunting species in conservation efforts (e.g. lions and wolves), and their recognition in structuring communities, the ecology of their cooperative hunting behavior is not well understood.
- The PI will answer the following questions using two models and a meta-analysis: (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?, and (4) Does the spread of cooperative hunting also select for reproductive skew?

Intellectual Merit

- Previous work on evolution of social traits in group-structured populations did not allow enough flexibility in group membership. The P.I. proposes a group-structured model with analytical, continuous time, dynamics in which predators can leave and join groups. A model of group formation originally developed for studying the coagulation and fragmentation of particles in chemistry was proposed as a model of animal group formation 1994 (Gueron and Levin) which allowed fission-fusion dynamics of groups, but has not been extended to the study of the ecology and evolution of social behavior until now .
- Previous predator-prey models where predators hunted in groups used allee effects for cooperation and did not account for both the impact of sharing and the benefits of group size on the ability of predators to capture larger types of prey, which the proposed models will address.
- Applying an ecological, niche-construction viewpoint to the study of different cooperative behaviors, which may help explain situations in which cooperation evolves even between group members who are not very related.

Broader Impacts

- Conservation needs better understanding of social behavior of predators
- Throughout the meta-analysis, the P.I. will mentor high school students

Project Description

Introduction

164 years have passed since Darwin admitted that altruism may be the one flaw in his theory of evolution. Cooperation is the donation of an aspect of an organism's survival, growth, or ability to reproduce in order to help another organism, and altruism is a type of cooperation in which the cooperative behavior does not result in the donor receiving a direct fitness benefit in return within its lifetime [28]. There are many types of cooperative behaviors that differ in the component of fitness being donated, which can be thought of as their ecological currency. These different types of cooperative behaviors may be the aspect of fitness which is donated or exchanged; three broad categories are fecundity, resources, or survival [26]. One type of cooperative behavior can, through its ecological currency, alter the environment and the altruistic species' social structure in a way that feeds back on the evolution of other cooperative traits with distinct ecological currencies; this process is called reciprocal niche construction [17]. For example, resource altruism has been hypothesized to decrease local competition between group members, making them more likely to help each other breed even if relatedness between group members is low [27]

However, exceedingly few theoretical or empirical studies have investigated the effects of niche construction of cooperative traits, nor the reciprocal niche construction that may allow high levels of cooperation between kin or even non-kin to evolve. This gap is not only a disservice to the field of evolutionary biologists studying the evolution of cooperation, but also to ecology and conservation. Many species that are considered to structure their local communities, such as sea otters [6, 7], orcas [6, 25], and wolves [5] are also extremely social, and of the few studies examining the topic, their social behavior can alter and be altered by their interactions with other species [14, 13, 8]. Very little modeling has studied the influence of the evolution of social behavior on the population dynamics of predators and prey. Previous work has examined how the evolution of social learning and cooperation influences prey choice and prey population dynamics in a one-predator, two-prey model where the predator population was held constant [3, 2, 4], and one model has examined the influence of social learning by predators in a one predator, one prey model where both populations changed [15]. Previous work on cooperation in predator-prey models have modeled cooperation as an allee effect, assuming the capture rate of prey is a function of predator density rather than group size [1, 21], even though studies of social species have largely been unable to observe population-level allee effects [16]. The only paper with a predator functional response that incorporated sharing and was a function of predator group size rather than predator population size, assumed that predator groups do not improve capture probability of prey [9].

Additionally, group structured-populations remain a challenge to ecological and evolutionary models of social behavior. Group-selection models have sought to examine how cooperative traits may spread by increasing the competitive advantage, and hence relative fitness, of groups with more cooperators, but these models generally do not both allow for group formation and for individuals to leave or join groups if it will increase their own fitness [22, 18]. However, many social predators are increasingly recognized to live in groups with flexible group membership [19, ?] (also unpublished observations from Adrian Treves of solves switching groups)

Here, the P.I. focuses on cooperative hunting and reproductive skew resulting from fecundity altruism. Cooperative hunting describes predators hunting a prey item as a group and sharing the resulting kill, and may be most advantageous if it allows predators to expand their niche by hunting prey they could not catch otherwise. Reproductive skew is the uneven distribution of resources among organisms. It can arise randomly [20, 23], but in many types of cooperative organisms, including ants [11] and hyenas [10], socially-enforced hierarchies generate extreme reproductive skew. Here, the P.I. aims to (1) understand how resource-based cooperation, and specifically cooperative hunting, influences and is influenced by prey abundance, (2) examine the feedback between cooperative hunting and the evolution of reproductive skew caused by fecundity altruism.

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 $x \in 1, 2, \dots, p$. Let $f(x, t)$ be the number of groups of size x , which for brevity is also written as $f(x)$, so that the portion of predators in a group of size x is $\bar{f}(x) = xf(x)/p$. The population dynamics of predators and prey are

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

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

$$\frac{dM_2}{dt} = g_2 M_2 \left(1 - \frac{M_2}{k_2}\right) - \sum_{x=1}^{x_m} f(x) Y_2(x, M_1, M_2) \quad (1c)$$

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

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

for $i = 1, 2$. The parameters are defined in Table 1. Importantly, the predator group size influences the capture probability $\alpha_i(x)$, which is the probability a predator captures prey i upon encounter (Fig. 1). However, the combination of parameter θ_i, s_i are not very intuitive for understanding how the capture probability responds to group size, especially since increasing θ_i, s_i also changes the capture probability of solitary predators. For $\alpha_i(1)$ the capture probability of prey i by solitary predators, $\theta_i = -\frac{\ln(\frac{1}{\alpha_i(1)} - 1)}{1 - s_i}$ is substituted into eq. 2.

Table 1: List of parameters used in Project 1

Parameter	Definition
b_i	Conversion of prey i caught to predators; $b_1 > 0$ and $0 < b_2 < b_1$
δ	Death rate of predators, i.e. the probability a predator dies per unit ecological time; $\delta > 0$
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; $\theta_2 \leq 0$
s_i	Critical group size for predators hunting prey type i , $s_i > 1$.
h_i	Handling time of prey type i
a_i	Attack rate on prey type i

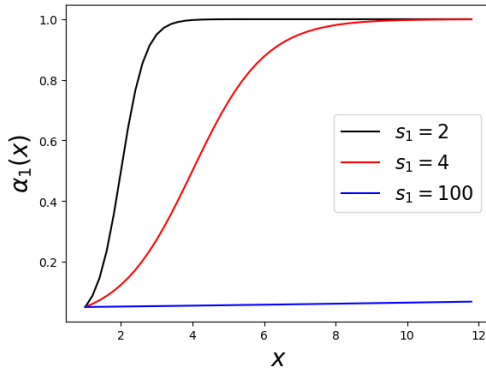


Figure 1: Capture probabilities of big prey if $\alpha_1(1) = 0.05$ for big prey and $\alpha_2(1) = 0.95$ for small prey, for different critical group sizes (s_1)

Predators may leave and join groups multiple times within their lifespan. The time constant for group dynamics is τ_x . While time for the population dynamics processes in system eqs. 1 is on the order of years or seasons, time for group dynamics may be on the order of days, so $\tau_x \ll 1$. Thus the group size distribution changes from the following processes: (1) solitary individuals join group of size x at rate $\psi(x)$, (2) individuals leave groups of size x at rate $\phi(x)$, (3) Individuals die at rate $\delta\tau_x$, the death rate relative to the time scale of group dynamics, and (4) individuals are born at a rate that is the yield from hunting, adjusted for the group formation time scale, i.e. $\tau_x f(x)\pi(x)$, where $\pi(x) = b_1 Y_1(x) + b_2 Y_2(x)$ is the yield from hunting. After birth, offspring

initially are in their natal group unless they are born in a group of the maximum group size, in which case they become solitary. The master equations for the number of solitary individuals, the number of groups of size 2, and number of groups of size $x \geq 2$, are, respectively,

$$\tau_x \frac{\partial f(1)}{\partial t} = + \underbrace{2 \cdot f(2)\phi(2)}_{\text{groups of 2 split to two solitaires}} + \underbrace{\sum_{x=3}^{x_m} f(x)\phi(x)}_{\text{individuals leave larger groups}} - \underbrace{f(1) \sum_{x=2}^{x_m} \psi(x-1)}_{\text{solitaires join groups}} + \underbrace{\tau_x \{f(x_m)\pi(x_m) - f(1)\pi(1) + \delta [2f(2) - f(1)]\}}_{\text{births and deaths}}, \quad (3)$$

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$$\tau_x \frac{\partial f(2)}{\partial t} = - \underbrace{f(2)\phi(2)}_{\text{an individual leaves}} - \underbrace{f(2)\psi(2)}_{\text{growing to larger group}} + \frac{1}{2} \underbrace{f(1)\psi(1)}_{\text{solitaires forming dyads}} + \underbrace{f(3)\phi(3)}_{\text{a member leaves a larger group}} + \underbrace{\tau_x \{f(1)\pi(1) - f(2)\pi(2) + \delta [3f(3) - 2f(2)]\}}_{\text{births and deaths}}, \quad (4)$$

and for $x > 2$,

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

Let $S(x, y)$ be the best response function modeling the probability a decision-maker will transition 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 the per capita fitness difference $\frac{1}{x}\pi(x) - \frac{1}{y}\pi(y)$ increases. We model this choice using Tullock's contest success function [24], i.e.,

$$S(x, y) = \frac{\left(\frac{1}{x}\pi(x)\right)^d}{\left(\frac{1}{x}\pi(x)\right)^d + \left(\frac{1}{y}\pi(y)\right)^d} \quad (6)$$

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

$$\psi(x) = \begin{cases} [f(1) - 1] S(2, 1) & \text{if } x = 1 \text{ and } f(x) \geq 1 \\ f(1)S(x+1, 1) & \text{if } 1 < x \leq x_m - 1 \\ 0 & \text{otherwise,} \end{cases} \quad (7)$$

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 $x \leq x_m$.

This model can be partially non-dimensionalized, scaling the population sizes of big prey and small prey by their carrying capacities, so $N_1 = M_1/k_1$ for big prey and $N_2 = M_2/k_2$ for small prey. The population time-scale constant is $\hat{t} = g_1 + g_2 + \delta$, with non-dimensionalized time $T = t\hat{t}$ and the group dynamics time constant $T_x = \hat{t}\tau_x$. For $\xi = \hat{t}/(a_1 + a_2)$ the ratio of the predation-independent growth rates to the attack rates, the predator population is scaled to $P = p/\xi$ and the number of groups of size x is $F(x) = f(x)/\xi$. The new parameters are $\eta_i = g_i/\hat{t}$, $A_1 = a_1/(a_1 + 1_2)$, $\beta_i = a_i b_i k_i / \hat{t}$, and $H_i = a_i h_i k_i$. It is not useful to non-dimensionalize group size, x .

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 restricting 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 of prey selects for more cooperation by examining whether increasing growth rates of big prey expected group size to which a randomly selected predator belongs, $\bar{x} = \sum x \tilde{f}(x)$, by calculating $\frac{\partial \bar{x}}{\partial N_1}$ at the equilibrium, and by testing whether an increase in the growth rate of big prey, g_1 , leads to an increase in \bar{x} . 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 [12], between prey types, and whether 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.

Cooperative Hunting

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, but predator grouping increases the capture probability of big prey. The rate at which predator groups catch prey is similar to eq. 2 but $M_1, M_2 = 1$. Since there should be a trade-off between the amount of effort spent on one prey on the amount of effort available on the other prey, there is handling time for prey, but since handling time is not the focus, it is set to $h_1 = h_2 = h$. Additionally, to increase tractability the attack rates of both prey are the same and set at $a_1 = a_2 = 1$. Thus if all predators spend all their time foraging, then the group's yield (i.e. number of offspring) from hunting is

$$\pi(x) = \frac{b_1 \alpha_1(x) + b_2 \alpha_2(x)}{1 + h \alpha_1(x) + h \alpha_2(x)} \quad \text{for } \alpha_i(x) = \frac{1}{1 + e^{-\theta_i(x-s_i)}}. \quad (8)$$

Reproductive Skew

Reproductive skew will be represented in one of the following ways:

1. Public Goods Game: If the yield from prey is first split evenly, such that each individual in a group of size x receives yield $\frac{1}{x}\pi(x)$, and subordinates sacrifice a portion γ to the dominant, then the direct fitness of subordinates is $w_s(x) = \frac{\pi(x)}{x}(1 - \gamma)$ and that of the dominant is $u\frac{1}{x}\pi(x)[1 + \gamma(x - 1)]$, where $u > 1$ is a multiplication factor.
2. Division of Time Budgets: Predators split their time between foraging and reproducing, so by sacrificing a portion of their reproductive effort γ , subordinates also decrease their time reproducing by γ and thus spend more time hunting. The dominant decreases its time hunting by γ for each subordinate in the group. Thus as γ increases, the expected number of hunters that are actively hunting at any given moment of time increases.

Group Fission And Fusion

As in project 1, $f(x)$ is the number of groups of size x . Here, offspring initially stay in their native group. One individual in a group is a dominant and the rest are subordinates, but every group member has a uniform probability $1/x$ of being a dominant. As in Project 1, $\psi(x), \phi(x)$ are the rates at which predators join and leave a group, respectively. If predators are able to freely leave and join groups, then when a predator is deciding to join or leave a group, it compares its solitary fitness to the expected fitness in the group. If groups control whether predators can stay or join, then a predator leaves a group if the group's fitness increases by decreasing group size. A predator joins a group if its own fitness increases by joining the group and if the group's fitness increases by augmenting group size. Since this model does not focus on population dynamics, population size is held constant by balancing the birth rate of the population with the death rate. For $W(x)$ the total birth rate of a group of size x , then because $\sum_x f(x)W(x)$ is the overall birth rate of the population, the per-capita death rate is $\delta = \frac{1}{p} \sum_x f(x)\bar{w}(x)$ for $p = \sum_x xf(x)$ the constant population size.

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

This project explores trends in the social behavior and ecology of Carnivora with the aim of comparing the ecology and social behaviors of predators that hunt alone, those that hunt in groups but do not cooperate, and those that both hunt in groups and cooperate. Previous work exploring the diversity of social hunting strategies HAS SELECTED PREDATORS THAT ARE SOCIAL, COMPARING THEM TO A FEW SPECIES THAT ARE SOLITARY?? In particular, the P.I.'s intend to investigate whether predators that hunt cooperatively also breed cooperatively. The P.I.'s focus on Carnivora because it is a relatively small order (only around 270 species) that contains well known examples of cooperative hunters, solitary hunters, and cooperative breeders, including some species that use a mix of solitary hunting and cooperative hunting.

The P.I. will mentor a high school student to collect the following information, where available, on species of carnivora:

- 184 1. **Group Hunting Characteristics** - Whether the predator hunts in groups, the size of those
185 groups, the degree of collaboration and sharing while hunting, and whether both sexes or
186 just one sex hunts in groups.
- 187 2. **Cooperative Breeding** - Whether females raise young in groups (i.e., in the presence of
188 adult conspecifics), the degree of reproductive skew in groups, whether some adults help
189 rear the young of other adults, and the presence of infanticide in groups.
- 190 3. **Prey characteristics** - The types of prey hunted in groups and alone, the size of the prey
191 relative to the predators, and the sociality of the prey.

192 A particular goal of this research is to help parametrize the model? For instance to understand
193 relatedness in cooperative hunting groups.

194 **Broader Impacts**

196 **Results From Prior NSF Support**

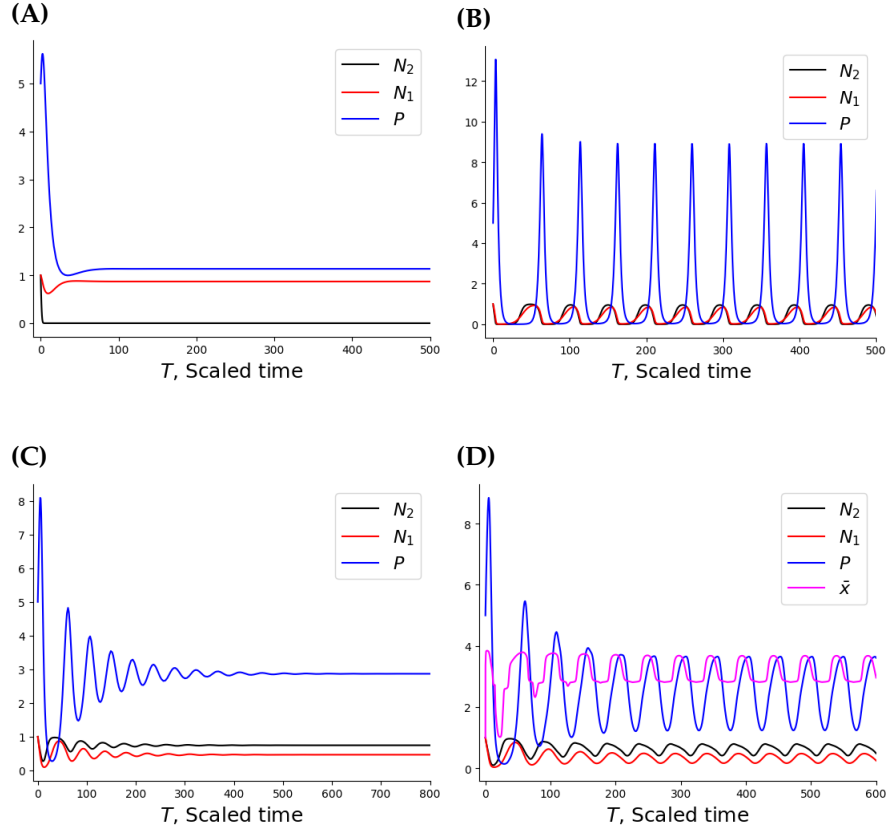


Figure 2: A comparison of population dynamics for all groups of the same size (panels (A) - (C)) and for a trajectory in which groups changing (panell (D)). For all panels, the parameters are $\xi = 2, \eta_1 = 0.2, \eta_2 = 0.4, A_1 = 0.5, \beta_1 = 10, \beta_2 = 1, H_1 = 2, H_2 = 2, \alpha_1(1) = 0.05, s_1 = 2$, and $\alpha_2(x) = 0.95$ is constant, and the initial scaled population sizes are $P(0) = 5, N_1(0) = N_2(0) = 1$. For panels (A) - (D), the scaled population sizes of predators, P , big prey, N_1 , and small prey N_2 , are shown in relation to scaled time, T , but in panel (D), the change in the expected group size that a randomly selected predator is part of, \bar{x} is also shown versus time, T . For panels (A) - (C), the group size of predators if $x = 1, 2$, and 4 respectively. For the trajectory shown in panels (D), the scaled group dynamics time constant is $T_x = 0.01$, and all predators are initially solitary.

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