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TWO HABITATS AND A PREDATOR SWITCHING MODEL WITH GROUP DEFENSE

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ABSTRACT

A model which describes the interaction of one predator with two prey species is considered. Due to large size, prey species have the ability of group defense. Therefore, the predator will be attracting toward that habitats where prey are less in number due to change in seasonal conditions. The stability analysis is carried out for a critical point of the system where all species co-exist. Using rate of conversion of the prey to predator as bifurcation parameter, conditions for a Hopf bifurcation to occur are derived.

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INTRODUCTION

In predator-prey environment, when a prey species of small size with little defense capability with respect to predator, like small Dik-dik, the predator prefers to catch prey species in a habitat where they are in abundance. All small species avoid to detected by predators therefore, they like to lives in less cohesive and coordinated feeding groups since they have to search for scarce, scattered food items of high quality like new leaves, seeds, and fruits and are also unable to communicate in vegetation. When the prey population in habitat starts declining due to heavy predation the predator switches over to other habitat where the prey species is in large number due to light predation. Because they are small and vulnerable, they switch and feed cautiously and slowly and never move far from cover. The size of the territory is presumably determined by the area that a pair can defend and by the availability of suitable food at the season of greatest scarcity. These species characteristically remain in one vegetation type in all seasons.

Group defense is a term used to describe a phenomenon whereby predation is decreased or even prevented altogether by the ability of the pre population to better defend themselves when their number is large. Major predators of zebra, buffalo, kongoni, toki and Thomson's gazelle are hyena, wild dog, lion, leopard and cheetahs. They form groups for defense against predators and more likely depend upon self-defense, group defense, group alertness within a group and speed, to avoid being killed by a predator. Therefore, such groups are more likely to be found where visual communication is favored and where individuals can conform to the group, speed, and direction of movement. Unless the group remains cohesive and coordinated, the individual risks becoming an outstanding target. This assumes that the predators do not search out areas with very large prey density. Pairs of musk-oxen can be successfully attacked by wolves but groups are rarely attacked. There are many examples of group defense (Yang and Huphrey, 1975; May and Robinson, 1985; Holmes and Bethel, 1972) and references there in. Herds remain well coordinated even under attack and individuals may benefit from the alertness and communication within the herd. Individuals tend to conform with their neighbor activities and many hundreds even thousands of wildebeest can coordinate rapidly in response to

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an alarm. Large groups also benefit from increased ability probability of detection of predators. The hunting success of lions decline if the group size of prey is large. Cheetah prefers to hunt single animals. Coursing predators select less healthy, old, sick and young prey and those who have lost their herds during migrations due to various reasons. Animals in poor condition and without group may reduce vigilance rates. In predator-prey environment, the predator prefers to feed-itself in a habitat or some duration and changes its preference to another habitat. This preferential phenomenon of change of habitats from one to other is called switching. There may be several reasons of switching of predators. For example – predator prefers to catch prey species in a habitat where they are in abundance but after some duration of heavy predation, when the prey species population starts declining, the predator changes its preference to another habitat etc., The mathematical models that have generally been proposed with switching are those involving interaction of one predator with two prey species (Tansky, 1978; Prajneshu and Holgate, 1987; Khan *et al.* (1996, 1994, 1998); Song *et al.* (2001), Hashem *et. al* (2013)), and two predator and two species Khan *et al.* (2010).

Large prey species like wildebeest, Zebra, Thomson's gazelle feed upon abundant, evenly dispersed, easily find food items. Food items of low quality (nature leaves, stems) are much more in abundant than those of high quality within selected habitats and so they form huge and cohesive groups. Seasonal condition of heavy rain storms dry season and other harsh environment force wildlife to migrate to other habitats for better condition, food and surface water. Usually wild life animals' distillate near permanent water during dry periods and disperse into neighboring dry habitat during wet periods. With the advent of dry weather the wildebeest return to their dry seasons range because grass growth on the wet seasons range stops after a few days without rain, and there remains almost no standing crop as a for reservoir. Free standing water is also largely absent from this area. Wildebeests are thus forced to return to their dry season range which maintains green leaf for a long period and retains substantial reservoir of grass sward due to light grazing pressure in the wet season. Free standing water is also available there in pools among major river systems. In this way herbivores maximize the growth potential of the vegetation through rotational grazing where the two concentration areas are sufficiently far apart the movements are called seasonal migration.

All of the migratory species (wildebeest, zebra, and Thomson's gazelle) show similar seasonal shifts in habitats, using short grassland in the south during wet season and tall grasslands in the north during dry season Pennywick (1975) and Maddock (1979). Their long range movements roughly correspond to seasonal transitions. In this paper, we have considered a system having a predator species interacting with same prey species in two habitats. Prey is able to migrate among two different habitats at some cost to the population in the sense that the probability of survival during a change of habitat may be less than one. The predator can feed on either habitat. The prey species in both habitats have the ability of group defense but it will be effective in the habitat where the population of prey is large. The predator will be attracted towards that habitat where the prey species are less in number. (Tansky, 1978) considered a general volterra type of two prey and of one predator mathematical model which has the switching property of predation of the following from

$$\frac{dx}{dt} = \left\{ r_1 - \frac{az}{1 + (y/x)^n} \right\} x,$$

$$\frac{dy}{dt} = \left\{ r_2 - \frac{bz}{1 + (y/x)^n} \right\} y,$$

$$\frac{dz}{dt} = -r_3 + \frac{a_1 xz}{1 + (y/x)^n} + \frac{a_2 yz}{1 + (y/x)^n}, \quad n = 1, 2, 3, \dots,$$

where x , y and z denote the abundance of two kinds of the prey species and predator species respectively. r_1 and r_2 are the specific growth rates of the prey species in the absence of predation and r_3 is the pre capita death rate of the predator. The functions

$$\frac{a}{1 + (y/x)^n} \quad \text{and} \quad \frac{b}{1 + (y/x)^n}$$

have a characteristic property of switching mechanism. The property rate that an individual of the prey species is attacked by a predator decreases when the population of that species becomes exceptional compared with the population of another prey species. This property is much amplified for large value of n . He studied the model with simplest form of the function for $n = 1$.

The model

The prey-predator model where the pre species exhibits group defense is of the form

$$\frac{dx_1}{dt} = \alpha_1 x_1 - \varepsilon_1 x_1 + \varepsilon_2 p_{21} x_2 - \frac{\beta_1 x_2 y}{1 + \left(\frac{x_1}{x_2}\right)^n},$$

$$\frac{dx_2}{dt} = \alpha_2 x_2 - \varepsilon_2 x_2 + \varepsilon_1 p_{12} x_1 - \frac{\beta_2 x_1 y}{1 + \left(\frac{x_2}{x_1}\right)^n}, \quad (1)$$

$$\frac{dy}{dt} = \left[-\mu + \frac{\delta_1 \beta_1 x_2^{n+1}}{x_1^n + x_2^n} + \frac{\delta_2 \beta_2 x_1^{n+1}}{x_1^n + x_2^n} \right] y,$$

with $x_1(0) > 0$, $x_2(0) > 0$, $y(0) > 0$.

x_i : represents the population of the prey in two different habitats

y : represents the population of predator species

β_i : measure the feeding rates of predator on the prey species in habitat 1 and habitat 2

δ_i : conversion rate of prey to predator

ε_i : inverse barrier strength in going out of the first habitat

p_{ij} : the probability of successful transition from i^{th} to j^{th} habitat ($i \neq j$)

α_i : pre capita birth rate of prey species in two different habitats

μ : the death rate of the predator

For $n = 1$, the case has been studied by Khan *et. al* (1998), where the relative abundance of the prey species has a simple multiplicative effect. For $n = 2$ the case has been studied by Khan *et. al.* (1999), for $n = 3$ the case has been studied by Hashem *et. al.* (2013), where the effect of relative density is stronger than the simple multiplicative. Here our aim is to generalize the results of the same model (Tansky, 1978; Ali *et al.*, 2013) for $n \geq 1$.

Stability of Equilibria

The non-zero equilibrium point of the system (1) is given by:

$$\bar{x}_1 = \frac{\mu \bar{x} (\bar{x}^n + 1)}{\delta_1 \beta_1 + \delta_2 \beta_2 \bar{x}^{n+1}},$$

$$\bar{x}_2 = \frac{\mu (\bar{x}^n + 1)}{\delta_1 \beta_1 + \delta_2 \beta_2 \bar{x}^{n+1}}, \quad (2)$$

$$\bar{y} = \frac{((\alpha_1 - \varepsilon_1) \bar{x} + \varepsilon_2 p_{21}) (\bar{x}^n + 1)}{\beta_1}.$$

Or

$$\bar{y} = \frac{((\alpha_2 - \varepsilon_2) + \varepsilon_1 p_{12} \bar{x}) (\bar{x}^n + 1)}{\beta_2 \bar{x}^{n+1}},$$

where $\bar{x} = \bar{x}_1 / \bar{x}_2$, is a real positive root of the following n^{th} order equation

$$\beta_2 (\alpha_1 - \varepsilon_1) \bar{x}^{n+2} + \beta_2 \varepsilon_2 p_{21} \bar{x}^{n+1} - \beta_1 \varepsilon_1 p_{12} \bar{x} - \beta_1 (\alpha_2 - \varepsilon_2) = 0. \quad (3)$$

For equilibrium values $(\bar{x}_1, \bar{x}_2, \bar{y})$ be a positive real root of the Eq. (3) must be bounded, therefore

$$\frac{\varepsilon_2 - \alpha_2}{\varepsilon_1 p_{12}} < \bar{x} < \frac{\varepsilon_2 p_{21}}{\varepsilon_1 - \alpha_1} \tag{4}$$

Let $\bar{E} = (\bar{x}_1, \bar{x}_2, \bar{y})$ denote the non-zero equilibrium point where $\bar{x}_1, \bar{x}_2, \bar{y} > 0$. We investigate the stability of \bar{E} and the bifurcation structure, particularly Hopf bifurcation, for the system (1), using δ_i (conversion rates of the prey u to the predator) as the bifurcation parameter. We first obtain the characteristic equation for the linearization of the system (1) near the equilibrium. We consider a small perturbation about the equilibrium value i.e. $x_1 = \bar{x}_1 + u, x_2 = \bar{x}_2 + v$ and $y = \bar{y} + w$. Substituting these values into the system (1) and neglecting the terms of second order in small quantities, we obtain the stability matrix equation

$$\begin{pmatrix} A - \mu & B & \frac{-\beta_1 \bar{x}_2^{n+1}}{\bar{x}_1^n + \bar{x}_2^n} \\ C & D - \mu & \frac{-\beta_2 \bar{x}_1^{n+1}}{\bar{x}_1^n + \bar{x}_2^n} \\ E & F & -\mu \end{pmatrix} = 0, \tag{5}$$

which leads to the eigenvalue equation

$$\mu^3 + a_1 \mu^2 + a_2 \mu + a_3 = 0, \tag{6}$$

where

$$a_1 = -(A + D),$$

$$a_2 = \frac{F\beta_2 \bar{x}_1^{n+1}}{\bar{x}_1^n + \bar{x}_2^n} + \frac{E\beta_1 \bar{x}_2^{n+1}}{\bar{x}_1^n + \bar{x}_2^n},$$

$$a_3 = -\left(\frac{DF\beta_1 \bar{x}_2^{n+2}}{\bar{x}_1(\bar{x}_1^n + \bar{x}_2^n)} + \frac{DE\beta_1 \bar{x}_2^{n+1}}{\bar{x}_1^n + \bar{x}_2^n} + \frac{AF\beta_2 \bar{x}_1^{n+1}}{\bar{x}_1^n + \bar{x}_2^n} + \frac{AE\beta_2 \bar{x}_1^{n+2}}{\bar{x}_2(\bar{x}_1^n + \bar{x}_2^n)} \right),$$

$$A = (\alpha_1 - \varepsilon_1) + \frac{n\bar{y}\beta_1 \bar{x}_1^{n-1} \bar{x}_2^{n+1}}{(\bar{x}_1^n + \bar{x}_2^n)^2},$$

$$B = -\frac{A\bar{x}_1}{\bar{x}_2} = \varepsilon_2 p_{21} + \frac{n\bar{y}\beta_1 \bar{x}_2^{2n}}{(\bar{x}_1^n + \bar{x}_2^n)^2} - \frac{(n+1)\bar{y}\beta_1 \bar{x}_2^n}{\bar{x}_1^n + \bar{x}_2^n}, \tag{7}$$

$$C = -\frac{D\bar{x}_2}{\bar{x}_1} = \varepsilon_1 p_{12} + \frac{n\bar{y}\beta_2 \bar{x}_1^{2n}}{(\bar{x}_1^n + \bar{x}_2^n)^2} - \frac{(n+1)\bar{y}\beta_2 \bar{x}_1^n}{\bar{x}_1^n + \bar{x}_2^n},$$

$$D = (\alpha_2 - \varepsilon_2) + \frac{n\bar{y}\beta_2 \bar{x}_1^{n+1} \bar{x}_2^{n-1}}{(\bar{x}_1^n + \bar{x}_2^n)^2},$$

$$E = \frac{(n+1)\bar{y}\delta_2 \beta_2 \bar{x}_1^n}{\bar{x}_1^n + \bar{x}_2^n} - \frac{n\bar{y}\delta_2 \beta_2 \bar{x}_1^{2n}}{(\bar{x}_1^n + \bar{x}_2^n)^2} - \frac{n\bar{y}\delta_1 \beta_1 \bar{x}_1^{n-1} \bar{x}_2^{n+1}}{(\bar{x}_1^n + \bar{x}_2^n)^2},$$

$$F = \frac{(n+1)\bar{y}\delta_1\beta_1\bar{x}_2^n}{\bar{x}_1^n + \bar{x}_2^n} - \frac{n\bar{y}\delta_1\beta_1\bar{x}_2^{2n}}{(\bar{x}_1^n + \bar{x}_2^n)^2} - \frac{n\bar{y}\delta_2\beta_2\bar{x}_1^{n+1}\bar{x}_2^{n-1}}{(\bar{x}_1^n + \bar{x}_2^n)^2}.$$

The Routh-Hurwitz stability criteria of eigenvalue equation (6) is $a_1 > 0$, $a_3 > 0$ and $a_1 a_2 > a_3$.

Hence, the equilibrium \bar{E} will be locally stable to small perturbation if it satisfies the following conditions

$$\alpha_1 + \alpha_2 + \frac{n\bar{x}_1^{n-1}\bar{x}_2^{n-1}}{(\bar{x}_1^n + \bar{x}_2^n)^2}(\beta_1\bar{x}_2^{n+1} + \beta_2\bar{x}_1^{n+1}) < \varepsilon_1 + \varepsilon_2, \quad (8)$$

$$(D\beta_1 + A\beta_2\bar{x}^{n+2})\left(E + \frac{F}{\bar{x}}\right) < 0,$$

and

$$(\beta_1 + \beta_2\bar{x}^{n+2})(AE\bar{x} + DF) < 0 \quad (9)$$

Stability of the equilibrium point depends upon the conditions (4) and (8) together with various parameters.

Hopf bifurcation analysis

We study the Hopf bifurcation for the system of (1) using δ_1 (rate of conversion of the prey in habitat 1 to the predator) as the bifurcation parameter. The eigenvalue equation (6) has purely imaginary roots if and only if $a_1 a_2 = a_3$ for some value of δ_1 (say $\delta_1 = \delta_1^*$). For $A < 0$, $D < 0$, $E > 0$ and $F > 0$; a_1, a_2, a_3 are positive. There exists δ_1^* such that $a_1 a_2 = a_3$. Therefore, there is only one value of δ_1 at which we have a bifurcation. For some $\varepsilon > 0$ for which $\delta_1^* - \varepsilon > 0$, there is a neighborhood of δ_1^* , say $(\delta_1^* - \varepsilon, \delta_1^* + \varepsilon)$ in which the eigenvalue equation (6) cannot have real positive roots. For $\delta_1 = \delta_1^*$, we have

$$(\mu^2 + a_2)(\mu + a_1) = 0, \quad (10)$$

which has the three roots

$$\mu_1 = i\sqrt{a_2}, \quad \mu_2 = -i\sqrt{a_2} \quad \text{and} \quad \mu_3 = -a_1.$$

The roots are in general of the form

$$\begin{aligned} \mu_1(\delta_1) &= u(\delta_1) + iv(\delta_1), \\ \mu_2(\delta_2) &= u(\delta_1) - iv(\delta_1), \\ \mu_3(\delta_1) &= -a_1(\delta_1). \end{aligned} \quad (11)$$

To apply the Hopf bifurcation theorem as stated in (Marsden and McCrachen, 1976), we need to verify the transversally condition

$$\frac{du}{d\delta_1} \Big|_{\delta_1=\delta_1^*} \neq 0. \quad (12)$$

Substituting $\mu_k(\delta_1) = u(\delta_1) + iv(\delta_1)$ into the equation (6) and differentiating the resulting equations with respect to δ_1 and setting $u = 0$ and $v(\delta_1) = \bar{v}_1$, we get

$$\begin{aligned} \frac{du}{d\delta_1}(-3\bar{v}_1^2 + a_2) + \frac{dv}{d\delta_1}(-2a_1\bar{v}_1) &= a_1'\bar{v}_1^2 - a_3', \\ \frac{du}{d\delta_1}(-2a_1\bar{v}_1) + \frac{dv}{d\delta_1}(-3\bar{v}_1^2 + a_2) &= -a_1'\bar{v}_1, \end{aligned} \quad (13)$$

where

$a_1' = \frac{da_1}{d\delta_1} = 0$ (because A and D are independent of δ_1). $a_2' = \frac{da_2}{d\delta_1}$ and $a_3' = \frac{da_3}{d\delta_1}$, \bar{x} is a real positive root of the equation (3) which is independent of δ_1 .

Solving for $\frac{du}{d\delta_1}$ and $\frac{dv}{d\delta_1}$, we have

$$\left. \frac{du}{d\delta_1} \right|_{\delta_1=\delta_1^*} = -\frac{2a_2(a_1a_2' - a_3')}{4a_2^2 + 4a_1^2a_2}. \quad (14)$$

To establish the Hopf bifurcation at $\delta_1 = \delta_1^*$, we need to show that

$$\left. \frac{du}{d\delta_1} \right|_{\delta_1=\delta_1^*} \neq 0, \text{ i.e. } a_1a_2' - a_3' \neq 0. \quad (15)$$

At $\delta_1 = \delta_1^*$, $a_1a_2 = a_3$; gives

$$(\beta_1 - \beta_2\bar{x}^{n+2})(AE\bar{x} - DF) = 0,$$

i.e.

$$\bar{x} = \frac{DF}{AE}. \quad (16)$$

Substituting the values of a_1, a_2' and a_3' in the equation (15) and using the equation (16), we get

$$a_1a_2' - a_3' = \frac{\bar{x}_2}{1 + \bar{x}^n} (\beta_1 - \beta_2\bar{x}^{n+2}) \left(\frac{D}{\bar{x}} \frac{dF}{d\delta_1} - A \frac{dE}{d\delta_1} \right),$$

where

$$\frac{D}{\bar{x}} \frac{dF}{d\delta_1} - A \frac{dE}{d\delta_1} = \frac{AE^2}{F} \frac{d(F/E)}{d\delta_1} < 0,$$

$$\text{i.e. } \left. \frac{du}{d\delta_1} \right|_{\delta_1=\delta_1^*} > 0,$$

provided $\bar{x}^{n+2} \neq \beta_1 / \beta_2$ and $\mu_3(\delta_1) = -a_1(\delta_1) \neq 0$.

We summarize the above results in the following theorem.

Theorem: Suppose $\bar{E} = (\bar{x}_1, \bar{x}_2, \bar{y})$ exists, $A < 0, D < 0, E > 0, F > 0$ and δ_1^* be a positive root of the equation $a_1 a_2 = a_3$, then a Hopf bifurcation occurs and δ_1 passes through δ_1^* provided $\beta_1 / \beta_2 \neq \bar{x}^{n+2}$.

Similar analysis can be carried out by varying δ_2 (rate of conversion of the prey in second habitat to the predator) and we shall get the similar results.

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