

The impact of behavioral plasticity at individual level on domestic cat population dynamics

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Abstract

An extension of a model studying the population dynamic consequences of intra-individual variability in behavior is presented. Individuals can adopt three different tactics: hawk, dove and bully. We consider a population of individuals that compete for some resources. The same individual experiences the different tactics in his life and it is assumed that the game is played at a fast time scale in comparison to population dynamics. This fast part of the model is coupled to a slow part, which describes the growth of each sub-population. By use of aggregation methods, we obtain an equation governing the total population at the slow time scale. This equation is a logistic one whose r and K parameters are related to the payoff of the tactics. The model is applied to the case of domestic cat populations. Results show that the highest population density corresponding to urban environment is reached when all individuals are bully. We also obtain a gradient from rural to urban environments, respectively corresponding to aggressive to non-aggressive individuals. The results of the model are consistent with empirical data: high-density populations of domestic cats are mainly bullies, whereas low-density populations are mainly hawks. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Aggregation methods; Hawk-dove-bully game; Logistic equation; Individual behavior; Domestic cat

1. Introduction

There has been an increasing awareness of the importance of individual heterogeneity in life his-

tory process to population dynamics. Models that explicitly reflect individual differences in age, size, and stage, have led to many advances in our understanding of how individual variability influences the dynamics of the whole population (Leslie, 1945; Lebreton, 1981; Metz and Diekman, 1986; Caswell, 1989).

Variability within one individual (both phenotypic plasticity and learned behavioral change) represents another important topic (Hayes and Jenkins, 1997). Some kinds of animals and some

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types of behaviors are modified by experience (learning), and also because individual characteristics change with time like body size. Males may adopt one tactic when they are young, or small, or socially subordinate, and another tactic when they are older, larger and dominant (Caro and Bateson, 1986). The tactic adopted may also depend on encounter event. As weight is generally important for the outcome of a fight, a male may adopt different tactics according to the relative size and strength of the male opponents, i.e. attack and fight or avoid the physical confrontation. Examples of behavior changing over time is widespread in mammal's taxa like, e.g. domestic cat *Felis catus* (Liberg, 1981), elephant seals *Mirounga angustirostris* (Haley et al., 1994), red deer *Cervus elaphus* (Clutton-Brock et al., 1982), pronghorn *Antilocapra americana* (Byers and Kitchen, 1988) or gray squirrels *Sciurus carolinensis* (Koprowski, 1993). The population level consequences of such plasticity in behavior has rarely been investigated in population dynamical models (Nisbet et al., 1989; Yoshimura and Clark, 1991; Clark and Yoshimura, 1993; Bjornstad and Hansen, 1994). This is due to the difficulty of dealing with complex models, and also because intra-individual behavioral variability has been too recently recognized as being an important task in population biology (Hayes and Jenkins, 1997; Holmes and Sherry, 1997).

Auger and Pontier (1998) presented a new approach of population modeling that can be used to investigate the influence of intra-individual variability in behavior on population dynamics. This approach is based on the coupling of a game model describing encounters at a fast time scale (e.g. the day) to a model describing the population dynamics at a slow time scale (e.g. the year). The model has been applied to the populations of domestic cat (*Felis catus*). While the results were in good agreement with empirical data, the game dynamics incorporated only two behavioral tactics and was too simple to account for all tactics that might be adopted by individuals. The aim of the present study is to incorporate in the original model more tactics. The present paper is thus a complement to the study of Auger and Pontier (1998).

The paper is organized as follows. In Section 2, we describe the main features of domestic cat populations. In Section 3, we extend the original model of Auger and Pontier (1998) to three tactics. In Section 4 a single equation governing the total population is constructed, which allows a clarifying study of the consequences of the model.

2. Population biology of domestic cats

The spatial and social organization of the domestic cat is subject to considerable flexibility. This flexibility is dependent on environmental factors such as food availability and habitat patchiness (Liberg and Sandell, 1988; Pontier, 1993). In rural areas where food is regularly distributed, cats live at low density (less than 200 cats/km²) in large slightly overlapping home-ranges. They are aggressive and fight for monopolizing food and mates (Liberg, 1981; Pontier and Natoli, 1996). The issue of fighting, at least in males, is largely influenced by their phenotypic features (Liberg, 1981). Age, experience, physical condition, body size, are all important variables in determining the behavioral tactic adopted by a cat at each encounter event (Liberg, 1981; Yamane et al., 1996). A low number of males, mostly the dominants successfully reproduce and their individual reproductive success is high (Say et al., 1999). In contrast, when food and shelters are clumped and locally abundant as in urban areas, cats live at very high densities (more than 2000 cats/km²) in multi-male–multifemale groups in small and largely overlapping home-ranges. Males in the group form a linear dominance hierarchy (Natoli and De Vito, 1991) based on age and size (Say et al., 1999). Cats are much less aggressive but defend their social position against any challenger. All members of the social group defend the common territory and may react aggressively towards any intruder (Natoli, 1985; Natoli and De Vito, 1991). There is no physical competition among males during the breeding season (Natoli and De Vito, 1991). A tactic consisting in monopolizing the access to a receptive female is no more possible due to the strong pressure of other cats. As a result, several males copulate with the same fe-

male at each oestrus period and a high rate of multiple paternity is found (Say et al., 1999). The reproductive success of dominant males is lower than in rural populations but higher than low ranking males (Say et al., 1999 and unpublished data).

3. Model of a population structured in hawk, dove, and bully individuals

3.1. Fast part: hawk-dove-bully game

We assume, as in the article by Auger and Pontier (1998), that males frequently encounter each other and compete for resources (food or mates). This process is going on at a fast time scale compared to the long term evolution of the population. We assume that three behavioral phenotypes, hawk (H), dove (D) and bully (B) are present within the population. Hawk individuals are always aggressive. Dove individuals are not aggressive and they never escalate. Bully individuals start by escalating but retreat if opponent escalates. These three behavioral phenotypes are assumed to be achievable to all individuals, whatever their genotypes. Individuals may choose these alternative tactics according to the conspecific encountered (physical strength, dominance rank of the opponent).

Let us denote x_H , x_D , and x_B the proportions of hawk, dove and bully males, with $x_H = n_H/n$, $x_D = n_D/n$ and $x_B = n_B/n$, where n_H , n_D and n_B are, respectively, the number of hawk, dove and bully males, and $n = n_H + n_D + n_B$ the total population. We call x the vector $(x_H, x_D, x_B)^T$, where u^T means the transpose of vector u .

Let A be the 3×3 matrix representing the payoff. Then the payoff of tactic I against tactic J is a_{IJ} , for $I, J \in \mathcal{A} = \{H, D, B\}$; the payoff to tactic I against population x is $\sum_{J \in \mathcal{A}} a_{IJ} x_J = (Ax)_I$; and the payoff to population x against itself is $\sum_{I \in \mathcal{A}} x_I (Ax)_I = xAx$.

We are using as A the following classical H-D-B payoff matrix (Zeeman, 1981; Maynard Smith, 1982):

$$A = \begin{pmatrix} \frac{G-C}{2} & G & G \\ 0 & \frac{G}{2} & 0 \\ 0 & G & \frac{G}{2} \end{pmatrix} \quad (1)$$

where G is the gain, C is the cost of injuries resulting of fightings between aggressive individuals.

The game dynamics, played at the fast time scale, is written according to the replicator equations, Hofbauer and Sigmund (1998), based upon the main hypothesis that the rate of growth of those playing tactic I is proportional to the advantage of I. By suitable choice of time scale we can write:

$$\begin{cases} \frac{dx_H}{dt} = x_H((Ax)_H - xAx) \\ \frac{dx_D}{dt} = x_D((Ax)_D - xAx) \\ \frac{dx_B}{dt} = x_B((Ax)_B - xAx) \end{cases} \quad (2)$$

These equations assume that an individual compares the gain of each pure tactic to the average gain. If a tactic leads to a larger payoff than the average one, the proportion of individuals of the population using this tactic is increasing. Replicator equation (Hofbauer and Sigmund, 1998) can thus conveniently be applied to solve the optimal proportions of individual tactics within the population; see also Cressman (1992) and Mesterton-Gibbons (1992) for game dynamics models.

The analysis of system (Eq. (2)), (Zeeman, 1981), in $\Delta = \{x \in \mathbb{R}^3: x_I \geq 0, \sum_I x_I = 1\}$, under a reasonable constraint ($G < C$) give us the existence of single point attractor, $(G/C, 0, 1 - G/C)^T$, which essentially determine the asymptotic behavior of solutions. Thus, we have a globally stable equilibrium, the polymorphism of G/C hawk and $1 - G/C$ bully tactic.

3.2. Slow part: demography

Each individual changes its tactics at a fast time scale according to the opponent. For each sub-population (H, D and B), the slow part which describes the growth of each sub-population is composed of two terms, a linear growth term and negative quadratic terms taking into account the issue of each type of encounter event (HH, HD, HB, DH, DD, DB, BH, BD, BB). Individuals are assumed to encounter at random. Thus, negative terms are proportional to the products of sub-populations involved in each encounter event. The growth of each sub-population is described as follows:

$$\begin{cases} \frac{dn_H}{dt} = \frac{1}{3}rn - n_H \sum_{J \in \mathcal{A}} k_{HJ}n_J \\ \frac{dn_D}{dt} = \frac{1}{3}rn - n_D \sum_{J \in \mathcal{A}} k_{DJ}n_J \\ \frac{dn_B}{dt} = \frac{1}{3}rn - n_B \sum_{J \in \mathcal{A}} k_{BJ}n_J \end{cases} \quad (3)$$

where r is the linear growth rate of each sub-population. As we have assumed that individuals frequently change tactics, H, D as well as B individuals contribute to the growth of each sub-population leading to the same linear growth term in system (Eq. (3)). The ratio three indicates that the new born individuals are initially equally distributed among the three types of individuals. The negative terms take into account the long term effects of encounters between individuals playing the same or different tactics (k_{IJ} , $I, J \in \mathcal{A}$) on the growth of the population. The parameters r and k_{IJ} are all non-negative.

3.3. The complete model

The complete model describes the sub-population Hawk, Dove, and Bully dynamics. It is obtained by coupling the two parts presented above:

$$\begin{cases} \varepsilon \frac{dn_H}{dt} = nx_H((Ax)_H - xAx) + \varepsilon \left(\frac{1}{3}rn - n_H \sum_{J \in \mathcal{A}} k_{HJ}n_J \right) \\ \varepsilon \frac{dn_D}{dt} = nx_D((Ax)_D - xAx) + \varepsilon \left(\frac{1}{3}rn - n_D \sum_{J \in \mathcal{A}} k_{DJ}n_J \right) \\ \varepsilon \frac{dn_B}{dt} = nx_B((Ax)_B - xAx) + \varepsilon \left(\frac{1}{3}rn - n_B \sum_{J \in \mathcal{A}} k_{BJ}n_J \right) \end{cases} \quad (4)$$

where ε is a small parameter taking into account the two different time scales involved in the system. The first terms in the rightmost side of system (Eq. (4)) represent the fast part, game dynamics, while the second terms are the slow part, demography dynamics. It must be noted that the fast part keeps invariant the total population n , i.e. game dynamics is responsible for the variation of the proportions of hawk, dove, and bully individuals but not of the total density. G represents the gain when an individual accesses to the resource and we assume r to be proportional to G .

$$r = \alpha G \quad (5)$$

where α is a positive parameter which represents the conversion rate of the resource into biomass. Interactions between individuals have negative effects on the long term growth of the total population. The parameters k_{IJ} are assumed to be proportional to the difference between the gain G that individuals would get if they had free access to the resource and the gain that they really obtain at the occasion of a given encounter, i.e. the coefficient of the game matrix, $A = (a_{IJ})$, associated to this particular encounter event. The parameters k_{IJ} of the model are thus the following ones:

$$k_{IJ} = \beta(G - a_{IJ}), \quad \text{for } I, J \in \mathcal{A}, \quad (6)$$

where β is a positive parameter which can be thought as an encounter rate. To give an example, when a hawk individual encounters a dove individual his payoff is G and the parameter k_{HD} equals zero, i.e. that particular encounter has no negative effect on the growth of its subpopula-

tion; in contrast, if a dove individual encounters a hawk individual its payoff is zero and then $k_{DH} = \beta G$, i.e. dove individuals have no access to resources which has a negative effect on the growth of their subpopulation. Substitution of the payoff matrix coefficients in (Eq. (6)) leads to:

$$\begin{aligned} k_{HH} &= \frac{1}{2}\beta(G + C) & k_{HD} &= 0 & k_{HB} &= 0 \\ k_{DH} &= \beta G & k_{DD} &= \frac{1}{2}\beta G & k_{DB} &= \beta G \\ k_{BH} &= \beta G & k_{BD} &= 0 & k_{BB} &= \frac{1}{2}\beta G \end{aligned} \quad (7)$$

We assume that the encounter rate depends on the gain and cost values as follows:

$$\beta = \gamma \frac{G}{C} \quad (8)$$

where γ is a positive constant. The interpretation of Eq. (8) is based upon the two following statements:

- if the gain is increasing it is more attractive to attempt to get it and thus the encounter rate is also increasing; and
- if the cost is increasing the risk from fights grows and consequently the encounter rate decreases.

4. Aggregated model for the total population

From the complete system (Eq. (4)), we apply aggregation methods to obtain an aggregated equation, i.e. a single differential equation governing the total population size n , and only depending on n . Aggregation methods permit to reduce a large system of equations involving different time scales into a smaller system with a few global variables. The method is based on perturbation technics (Hoppensteadt, 1966; Auger and Rousarie, 1994; Auger and Poggiale, 1995, 1996).

The aggregation of the complete model consists in supposing that the fast dynamics, game dynamics, has already attained its equilibrium, $(G/C, 0, 1 - G/C)^T$, so we can make the following substitutions in system (Eq. (4)):

$$n_H = \frac{G}{C}n, \quad n_D = 0 \quad \text{and} \quad n_B = \left(1 - \frac{G}{C}\right)n,$$

and then by adding up the three equations we obtain:

$$\begin{aligned} \frac{dn}{dt} &= \alpha Gn - \left[\frac{1}{2}\gamma \frac{G}{C}(G + C)\left(\frac{G}{C}\right)^2 + \gamma \frac{G}{C}\left(1 - \frac{G}{C}\right)\frac{G}{C} \right. \\ &\quad \left. + \frac{1}{2}\gamma \frac{G}{C}G\left(1 - \frac{G}{C}\right)^2 \right] n^2 \\ &= \alpha Gn - \frac{1}{2}\gamma \frac{G}{C}G\left(1 + \frac{G}{C}\right)n^2 \end{aligned}$$

that is

$$\frac{dn}{dt} = (\alpha G) \left(1 - \frac{n}{\frac{\gamma G(C + G)}{2\alpha C^2}} \right) n \quad (9)$$

which is a logistic type equation with carrying capacity

$$K = \frac{2\alpha C^2}{\gamma G(C + G)} = \frac{2\alpha}{\gamma \left(1 + \frac{G}{C}\right)\frac{G}{C}} \quad (10)$$

The rightmost side of last equality expresses the carrying capacity K in terms of the equilibrium proportion of hawk individual G/C which we denote x_H^* , and so we can write:

$$K = \frac{2\alpha}{\gamma(1 + x_H^*)x_H^*} \quad (11)$$

As in Eq. 16 of the model in Auger and Pontier (1998), the carrying capacity is a decreasing function of the hawk proportion in the population. But high density population (large K) is now associated to bully individuals instead of dove individuals and low density population (small K) is associated to hawk individuals. Another important difference comes from the fact that the carrying capacity is now inversely proportional to $(1 + x_H^*)x_H^*$. As $x_H^* \in (0, 1)$ then $K \in ((\alpha/\gamma), \infty)$, which makes possible a large domain of carrying capacity values. This is an important improvement because in the previous model the carrying capacity could only vary by a factor two.

5. Discussion and conclusion

Our aim was to draw some conclusions about the effect of some kind of behavioral interactions on population dynamics with domestic cat populations in mind. The relationship between the equilibrium density of a population and its degree of aggressiveness which was established for the model taking into account two tactics, hawk and dove (Auger and Pontier, 1998), has been generalized to the hawk-dove-bully game. We obtained the same relationship between the carrying capacity K and the hawk proportion, as in the classical hawk-dove game (Auger and Pontier, 1998), but the relationship occurred with a hawk-bully polymorphism instead of a hawk-dove polymorphism. Dove individuals disappear from the population. It must be noted that the results at low density remain unchanged in spite of the supplementary tactics considered (bully): individuals are always hawk at low density. This is in good agreement with observations: individuals are aggressive and defend their access to resource (food and mates) at low densities in the rural environment. The prediction that individuals are mostly dove at high density as it was found for the hawk-dove model (Auger and Pontier, 1998) is not realistic in the case of domestic cat populations. Individuals are much less aggressive at high densities (Natoli and De Vito, 1991). A number of case contests are solved without resort to physical violence at all. However, individuals in a group defend their social position by fighting with any challenger. They can also challenge the upper dominant individual. These two behaviors could be identified with bully tactic. They also drive away unknown intruders from the common territory. This may explain why hawk tactic persists within urban populations. Including bully tactic into the original model gave rise to a new qualitative prediction, which is more consistent with available empirical data. The results of the present model remain, of course, theoretical and have to be tested. Our model assume that individuals will choose among tactics according to the payoff for winning and the cost due to fight. When the payoff is large compared to the cost then individuals adopt a hawk tactic (rural environment)

whereas when the payoff is low compared to the cost then individuals are all bully (urban environment). Determining quantitatively this ratio in both types of populations (rural and urban) is likely to be difficult in domestic cat. However, Say et al. (1999) showed that the reproductive success of dominant males is lower in high density (urban) than in low density (rural) domestic cat populations. It is likely that the cost due to fighting also differ between the two kinds of population. Once defeated, individuals in the urban populations loose not only their social rank but also their priority to access to the resource. Finding another resource may be difficult because the distance among favorable patches may be high and cats may have to cross many heavily traffic roads (Pontier, 1993). Moreover an immigrant is not accepted by members of a social group (Natoli, 1985; Natoli and De Vito, 1991; Say et al., 1999). Such difficulties do not exist in the rural environment where food is evenly distributed (Liberg, 1981). Loosing a fight beyond the cost due to injury may have a larger effect on lifetime fitness of individuals in the urban than in the rural environment.

As we have shown in this work, the aggregation method provides an efficient tool for describing in a relatively simple way the dynamics of a population whose individuals adopt different behavioral tactics in their life, the probability of adopting one tactic depending on density. The technique for analyzing the influence of intra-individual change in behavior on population dynamics we present here offer several advantages: (i) it takes into account different time scales appropriate to describe biological phenomenon (the day for behavioral interactions versus the year for population dynamics) (ii) it permits to explore several types of behaviors (e.g. foraging, breeding tactics), and different models for describing population dynamics, in regard to the population and situation being modelled. This requires to accumulate detailed information on numbers and density in populations monitored over long periods (Caro and Bateson, 1986). We have used this approach for domestic cats, but this technique is relevant for many taxa and a large variety of situations. We believe that the influence of intra-individual

variation in behavior on population dynamics is a biological important issue that deserves further theoretical and empirical research.

In our future work, we will deal with both intra- and inter-individual variation in behavior due to genetic differences (Caro and Bateson, 1986). Some individuals may adopt alternative behavioral tactics for life because of genetic differences. Genetic change is observed in concomitance with density change in domestic cat populations (Symonds and Lloyd, 1987; Pontier et al., 1995). There is also convincing evidence for genetic variation in behavior in domestic cat (Pontier et al., 1995, 1998). Cats carrying the orange allele may behave aggressively whatever the ecological conditions, while non-orange individuals have a more flexible behavior: either aggressive at low density, or social at high density. The frequency of the orange allele is very low (less than 10%) or even absent in urban environments, while it can reach high frequencies in the rural environment (up to 30%; Lloyd and Todd, 1989; Pontier et al., 1995). Our approach would permit to incorporate genetic and environmental influence in behavioral variation within and among individuals to further analyze the persistence of orange allele with density change. Next, our work will extend the results of the simplest population dynamical model to sex- and age-structured populations.

Acknowledgements

We are grateful to Drs D. Allainé, E. Fromont, J.-M. Gaillard, S. Charles and N. Bahi-Jaber for their constructive comments on a previous draft of the manuscript. This work is part of a contract with the CNRS (Program populations fragmentées, extinctions, sélection d'habitat et biologie de la conservation). This work was partly supported by the grant (null) Proyecto PSPGC PB98-0702.

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