



A study of prey–predator relations for mammals

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Abstract

In this paper, we present a prey–predator nonlinear model for mammals, consisting of large- and small-size prey species with group defence, in a partially protected habitat. If the prey size is small, then it is more prone to the predator at higher densities. Conversely, large prey size at higher densities tend to develop group defence. Therefore, the predator will be attracted towards that area where prey are less in number. A new physical constant has been introduced into the radiation-type condition on that part of the boundary where interaction between prey and predator takes place. This constant allows us to efficiently model group defence capabilities of the herds and its numerical values have to be determined for different pairs of prey–predator species from field observations. A way of measuring the constants involved in the model is suggested. Numerical results are provided and thoroughly discussed for a habitat of circular shape. The obtained results show that in the region away from the protected area, the density of large-size prey species is higher than that of small-size prey species, a fact that is in accordance with observations.

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1. Introduction

In a predator–prey environment, there are many mathematical models in the literature on selective predation, where the predator prefers to eat the prey species according to age, size, weight, number, etc. A predator prefers to catch a prey species that is most abundant, when the prey species is relatively smaller in size with little or insignificant defence capability with respect to the predator species, such as small antelopes, voles, dik-diks, and the predators are cruising (which move to locate the prey species). Smaller species are vulnerable to a greater range of predator species and are less likely to defend themselves against, or to outrun, predators. All small species avoid being detected by predators. Smaller species live singly or in pairs and find their resources within a defended territory. Because they are small and vulnerable, they move 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 all season.

Ruxton and Lima (1997) studied a predator–prey model where prey species are divided into breeder and suppressor classes. To avoid predation, it has been suggested that certain small mammals suppress breeding in response to strong predation pressure because non-breeding individuals have a better chance of avoiding predation than those in a reproductive stage. It has been suggested that breeding suppression is an adaptive mechanism of prey individuals to avoid predation (Magnhagen, 1991) and, specifically, that this phenomenon could explain at least some properties of Fennoscandian vole cycles (Ylönen, 1994). Several recent papers report that the presence of predators can induce a marked reduction in reproduction in several boreal mammals. Lima (1997) and Ylönen (1994) argued that predator-induced breeding suppression enhances survival of non-reproductive females during high predation and after which their reproduction efforts would be more successful.

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Large prey species like wildebeests, zebras and Thomson's gazelles feed upon abundant, evenly dispersed, easily found food items. Food items of low quality (natural leaves, stems) are much more abundant than those of high quality within selected habitats and so they form huge and cohesive groups. Large herd formers are more likely dependent upon self-defence and group defence, to avoid being killed by predators. Group defence is a term used to describe a phenomenon whereby predation is decreased or even prevented altogether by the ability of the prey population to better defend themselves when their number is large (see Hamilton (1971) for more details). The predators do not seek out areas with very large prey density (Schaller, 1972). Pairs of musk-oxen can be successfully attacked by wolves, but groups are rarely attacked (Tener, 1965). There are many examples of group defence (Yang and Humphrey, 1975; May and Robinson, 1985; Homes and Bethel, 1972). Herds remain well coordinated, even under attack, and individuals may benefit from the alertness and communication. Individuals tend to conform with their neighbour's activities and many hundreds, even thousands of wildebeests can coordinate rapidly in response to an alarm. Large groups also benefit from increased probability of detection of predators. The hunting success of lions decline if the group size of prey is large (Van Orsdol, 1984). Cheetahs prefer to hunt single animals.

The mathematical models involving predator and prey species interactions in which the predator feeds more intensively on the more abundant species, i.e. prey species is of small size with insignificant defence capability have been generally studied. One can refer to Holling (1961), Takahashi (1964), Murdoch and Qaten (1975), Roughgarden and Feldman (1975), Tansky (1976), Prajneshu and Holgate (1987), McNair (1987) and Khan et al. (1994). Freedman and Wolkowicz (1986); Freedman and Quan (1988); Ruan and Freedman (1991) have studied mathematical models for a prey–predator system in which the prey population exhibits group defence. Khan et al. (1998) have analysed a switching model with two habitats and a predator involving group defence.

In contrast to the usual prey–predator problems, which usually consider a certain process in time, thus leading to ordinary differential equations, the present paper is concerned with the investigation of the phenomenon of group defense in a certain type of animal community. This basically requires the consideration of a two-dimensional habitat and a certain density function, u say, the values of which vary from location to location, allowing for different concentrations of the prey. This non-uniformity of the density is described in mathematical terminology by the gradient vector of the density function. Another useful ingredient to be taken into consideration is the density flux vector

Ω , which must be related to the density function in the same way as the heat flow vector is related to the temperature as stated by the celebrated Fourier law for heat conduction in its simplest form in classical thermodynamics, $\Omega = -\mathbf{K} \text{grad } u$, where \mathbf{K} is a certain physical constant. The most direct implication of such a law is that the prey community, if left to itself without any interference by external agents, would naturally tend to redistribute itself uniformly over the land. Now, this density flux vector in the steady state, in which we are presently concerned, must satisfy a certain conservation law, expressed as $\text{div } \Omega = 0$. Such a law simply means that the number of animals within a certain closed boundary can change by a certain amount only if there is transport of the same amount of animals through the boundary. Combining the last two equations, one arrives at the conclusion that the density function in the steady state satisfies Laplace's equation at every point of the habitat.

In this paper, we study a system having a predator species interacting with prey species of small or large sizes. We are assuming that the prey species herds are living in a partially protected habitat with boundary of arbitrary shape. Wildlife animals, specially small-size prey species, remain concentrated near the region where they get maximum protection from predator species. Usually, these areas are covered by dense vegetation, broken terrains or bounded by a river. We are assuming that part of the boundary of the habitat is protected from the predator attack. Predator species attack prey species from the remaining part of the boundary. We also make a number of other important assumptions. The first of these is that predators adjacent to the interactive part of the boundary have constant (unit) density. The second assumption concerns the type of interaction between prey and predator. In analogy to heat conduction problems, this will be described by a radiation-type condition imposed on that part of the boundary through which hunting takes place. This law is taken to be nonlinear in the form

$$\frac{\partial u}{\partial n} = -q(u - 1),$$

with a “predator–prey interaction coefficient” q depending on the prey density at the boundary according to a parabolic law given by

$$q = q_0(1 - \alpha u^2),$$

where u denotes the prey density, n the direction of the outward normal to the boundary of the habitat in its interactive part and q_0, α are certain numerical constants depending on both the prey and the predator species. The constant α accounts for the group defence mechanism. These two constants have to be found from experimental data. Later on, a way is suggested for measuring them. For the sake of simplicity and in order to

concentrate on the “prey–predator” relation, we also assume that the “prey–predator” system is in a steady state, by which we suppose that the births and the deaths in the prey species occur equally in the habitat and that the prey density is governed by Laplace’s equation.

We believe that this is the first time such a population model has appeared in the literature. It allows us to account for the phenomenon of group defence in the prey species herds. It also efficiently explains that prey species of small size tends to remain away from the hunting area, while the prey species of large size (having group defence capability) is also found in hunting areas.

As an illustration, a boundary-value problem for a circular habitat has been solved in the case where half of the boundary is protected from the predator attacks. An approximate solution to the problem was found in the form of a Poincaré expansion in a small parameter, in conjunction with the well-known Boundary Collocation Method (Kolodziej and Kleiber, 1989). The method is simple, straightforward and generally produces highly accurate solutions. Moreover, it may be applied to other geometries of the boundary and with different boundary conditions. For complicated shapes, one may resort to a numerical approach. Graphs are presented for the prey density in the circular habitat, which show a comparison between different large-size prey species, different small-size prey species, as well as between large- and small-size prey species. Cases with other boundary geometries, like rectangular or elliptic boundaries, show comparable behaviour of the solution.

Taking into account our choices of the characteristic dimension of the habitat and the uniform predator density outside it, the presented field equations and boundary conditions are in dimensionless form.

2. Formulation of the problem

Consider a circle of unit radius and centre at O (Fig. 1) and let (r, θ) be polar coordinates in the plane of the

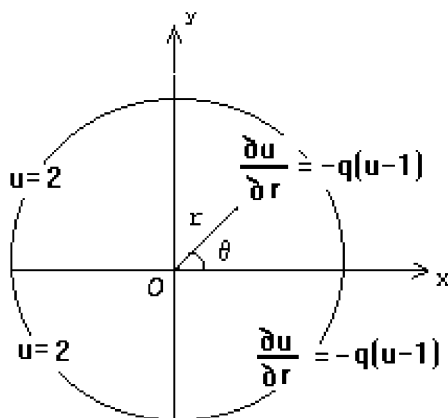


Fig. 1. Boundary conditions.

circle, with origin at O . Let $u(r, \theta)$ be the steady-state prey species density that lives inside the circular habitat. The variations of this function of space are conditioned by two factors: The reproduction and natural death, which may be described by source and sink terms, and the predation through the boundary, which is described by a radiation-type condition. A balance between these two factors may result in a steady-state prey distribution of density in the habitat. Thus, one may assume that u satisfies Laplace’s equation, on the basis of analogy with similar steady-state problems of fluid flow or heat conduction:

$$\Delta u = 0, \quad r < 1, \quad -\pi < \theta \leq \pi. \tag{1}$$

By setting to zero the density of sources and sinks inside the habitat, we have assumed that births and natural deaths occur equally there. Several authors have referred to the diffusion-type equation in solving prey–predator problems (cf. Pettet et al., 2000; Avila-Vales and Cantrell, 1997). For large time values, one may get steady-state solutions governed by Laplace’s equation.

The boundary conditions prevailing at the boundary of the circular habitat express two facts: (i) The constancy of the prey species density on that half of the boundary occupied by the river, where we have set $u = 2$. This condition implies that the reproduction and natural death take place only at that safe part of the boundary, which is in conformity with the discussion presented in the Introduction. (ii) A condition of interaction between the prey and the predator populations, the latter being taken to have a constant concentration (equal to unity) at all points adjacent to the second half of the circular boundary from the exterior. It will also be assumed that the rate at which the prey is attacked depends linearly on the difference of prey and predator concentrations near the boundary of the habitat. Thus, the boundary conditions may be written as in Fig. 1. In the dimensionless formulation adopted here, the unit value outside the habitat simply means that the density of the predator has been taken as a reference density:

$$\frac{\partial u}{\partial r} = -q(u - 1), \quad r = 1, \quad -\frac{\pi}{2} < \theta < \frac{\pi}{2}, \tag{2}$$

$$u = 2, \quad r = 1, \quad \frac{\pi}{2} < \theta < \frac{3\pi}{2}. \tag{3}$$

Coefficient q is the analogue of the well-known Biot constant in problems of heat conduction. For the present model, it represents the rate at which the prey species are attacked through half the boundary of the circular habitat. The values of this parameter will generally depend on the nature of the two interacting species. In order to take into account the group defence phenomenon of the prey species, it will now be considered that q is a function of u according to the

parabolic law

$$q = q_0(1 - \alpha u^2), \tag{4}$$

where q_0 and α are certain constants to be determined from observations. The constant q_0 assumes positive values, while α takes on positive values if the prey species is of large size, and negative values otherwise. The range of values $0 < \alpha \ll 1$ corresponds to the old, sick and those big prey species who have lost their herds. The range $\alpha < 0$ corresponds to small prey species. Smaller values of α within this range will correspond to weak or breeding small-size prey species. Figs. 2 and 3 show the variations of $q(u)$ for two values of α .

We thus have at hand a nonlinear, mixed boundary-value problem for the Laplace's equation in a circular region.

3. Method of solution

(see the appendix)

4. Numerical results

We have considered one value for the parameter q_0 ($q_0 = 0.1$), three cases with large prey size ($\alpha = 0.01, 0.05, 0.1$) and three other cases with small prey size ($\alpha = -0.01, -0.05, -0.1$). For each of these cases, we discuss the obtained results and present the graph for the steady-state distribution of the prey concentration inside their circular habitat. A comparison is then carried out between the different cases.

The points of the boundary at which the boundary conditions are enforced are uniformly distributed along the boundary, with

$$\theta_m = \frac{m\pi}{M}, \quad m = 0, 1, 2, \dots, M - 1. \tag{5}$$

This usually secures the best results. However, one may also attempt to improve the error in satisfying the boundary conditions by using optimization techniques. These are nonlinear and highly increase the cost of the solution.

For each chosen value of N , we have obtained the value for M which yields the minimal value for the error ε . Then we have found the critical value of N for the best result. The graphs are drawn according to the optimal values of N and M from the first two approximations only. An investigation of the higher order approximations does not affect the results significantly. Fig. 4 shows a typical curve for the error distribution $ER(\theta)$ obtained for $\alpha = 0.05$ (large prey species), $N = 92, M = 150$. One sees that $\varepsilon \approx 0.392 \times 10^{-3}$, which seems to be a sufficiently good accuracy in satisfying the boundary conditions. Other cases show the same level of accuracy.

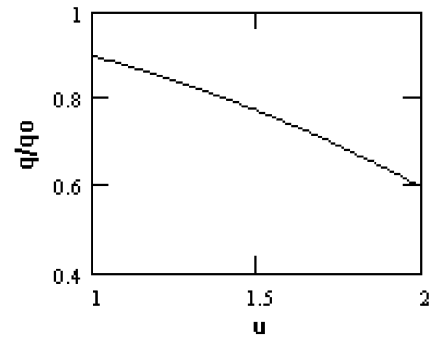


Fig. 2. Function q/q_0 for $\alpha = 0.1$ (large prey size).

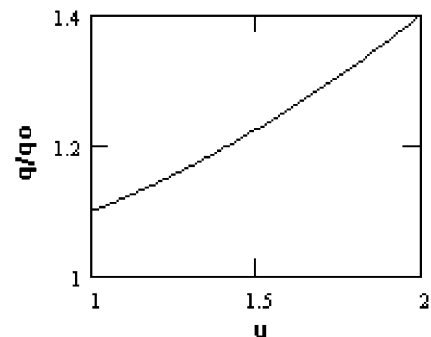


Fig. 3. Function q/q_0 for $\alpha = -0.1$ (small prey size).

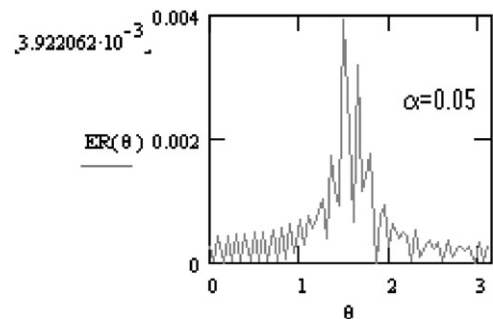


Fig. 4. Minimal error for $N = 92, M = 150$.

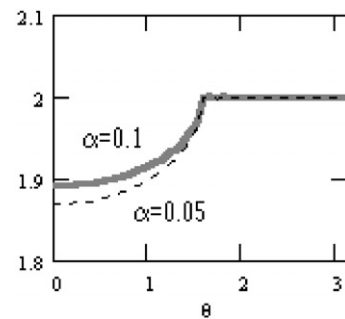


Fig. 5. $u(1.0, \theta)$ for large size prey.

Figs. 5–13 show the corresponding distributions of function u at different distances from the habitat centre ($r = 1.0, 0.9, 0.6$) for $0 \leq \theta \leq \pi$. Here, we have compared the densities of large prey sizes, of small prey sizes, as

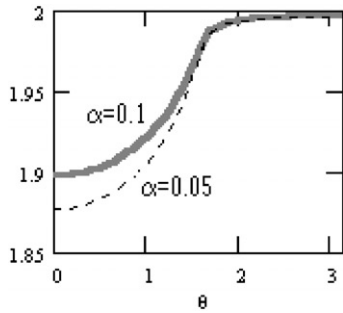


Fig. 6. $u(0.9, \theta)$ for large-size prey.

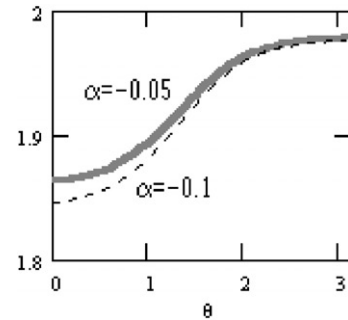


Fig. 10. $u(0.6, \theta)$ for small-size prey.

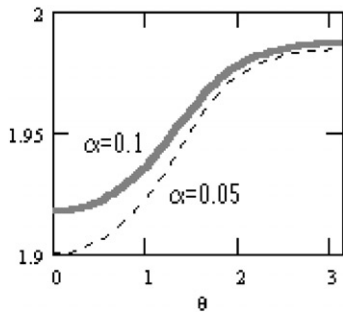


Fig. 7. $u(0.6, \theta)$ for large-size prey.

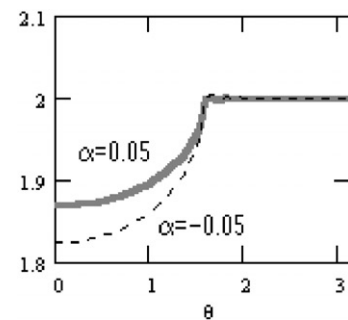


Fig. 11. $u(1.0, \theta)$ for large- and small-size prey.

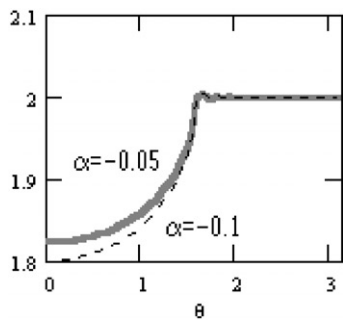


Fig. 8. $u(1.0, \theta)$ for small-size prey.

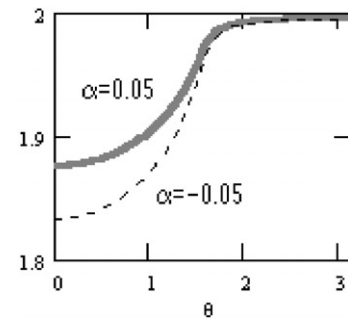


Fig. 12. $u(0.9, \theta)$ for large- and small-size prey.

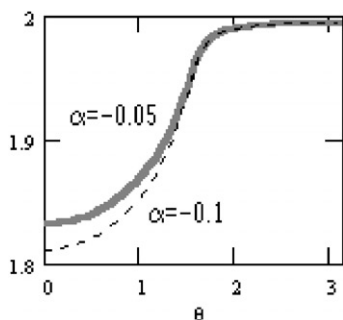


Fig. 9. $u(0.9, \theta)$ for small-size prey.

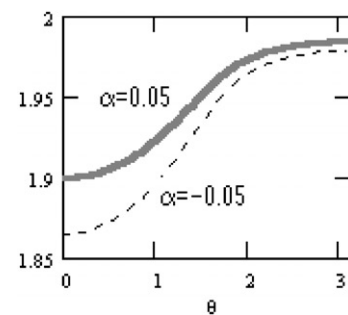


Fig. 13. $u(0.6, \theta)$ for large- and small-size prey.

well as between large and small prey sizes. The effect of group defence is most efficient in the vicinity of that portion of the boundary through which hunting takes place. This mechanism clearly enhances the prey density.

As one moves towards the safer area, the densities tend to be the same. As the centre of the habitat is approached, the densities tend to be more uniformly distributed.

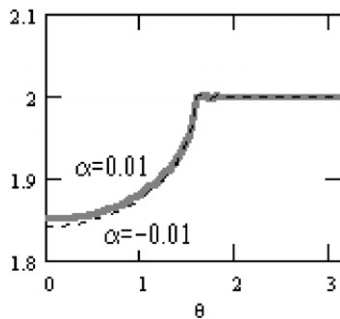


Fig. 14. $u(1.0, \theta)$ for $|\alpha| = 0.01$.

Of particular interest is Fig. 14, comparing densities of large size prey with low group defence capabilities ($\alpha = 0.01$) and small prey size ($\alpha = -0.01$). Here, the densities of both species near the boundary (and hence everywhere) become closer to each other, the difference tending to vanish as $\alpha \rightarrow \pm 0$. This means that large size prey species having no group defence capability behaves as small size prey species and their densities away from the protected area will almost be the same. Hence, the size of the prey species becomes immaterial.

5. Discussion and conclusions

We have studied a prey–predator system, consisting of prey species of mammals of both large and small sizes. The predator prefers to catch the prey species that is most abundant. Hence, instead of choosing individuals at random, a predator feeds preferentially on the most numerous prey species. This was often found to be the case where the prey species is relatively small in size with little or insignificant defence capability with respect to the predator species. These small prey species live in a less cohesive and coordinated feeding groups. Certain small mammals suppress breeding in response to strong predation pressure because non-reproductive females experience enhanced survival during high predation than in a reproductive state. Prey species of large sizes have the advantage of group defence but it will be effective when the population of prey species is large. They are rarely attacked by the predator when they are in large numbers.

The aim of the present work is to model this phenomenon of group defence. For this, we introduced a nonlinear relation that regulates the rate of predation at the boundary of the prey habitat. This law is analogous to the well-known radiation condition in problems of heat conduction, but with interaction constant depending on the density of the prey species at the boundary of their habitat. The two constants appearing in this law could be measured experimentally from two sets of measurements for the same given types of prey species and predator species. For this, one has

only to evaluate the prey densities at two nearby locations, one of them at the boundary of the habitat and the other in its interior, in such a way that the line joining the two positions is perpendicular to the boundary line. This would estimate the normal rate of change of the density at the boundary of the habitat.

In order to focus on the phenomenon under consideration, we restricted our analysis to the steady-state case and to a circular habitat. One half boundary of the habitat is bounded by a river or covered by high vegetation, broken terrains, which provide a secure environment for hiding, reproduction and maximum protection from predator species. Predators can attack from a certain number of places from the second half of the boundary of the habitat. The circular form and the used boundary conditions are not at all restrictive and any other forms of the habitat and of the boundary conditions may equally well be considered on the same mathematical basis. We found that the density of the small-size prey species is lower in the hunting area, than that of large prey species. The density of healthy and non-reproductive large-size prey species is higher in the hunting region than that of old, sick and those who have lost their herds. Our model explains this behaviour effectively. It is also observed that if the large-size prey species has low group defence capability, then it almost behaves like small-size prey species, the densities of both in the habitat becoming almost equal. However, we hope that the results and methodological framework outlined here will provide a useful tool for others to investigate the consequences for particular real systems. In particular, observations should be carried out in order to evaluate the physical constants implicated in the model.

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Appendix

If $|\alpha| < 1$, we may look for an approximate solution to the problem as a Poincaré expansion in the parameter α in the form

$$u = u_0 + \alpha u_1 + \alpha^2 u_2 + \dots, \quad (\text{A.1})$$

where u_i , $i = 0, 1, 2, \dots$, satisfy Laplace’s equation in the circular domain. Substituting into the boundary conditions (2),(3) and comparing the terms with the same order in α , one obtains the boundary conditions for the successive approximations to any desired order. For example, we get the following two sets of boundary conditions for u_0 and u_1 :

$$\frac{\partial u_0}{\partial r} = -q_0(u_0 - 1), \quad r = 1, -\frac{\pi}{2} < \theta < \frac{\pi}{2}, \tag{A.2}$$

$$u_0 = 2, \quad r = 1, \frac{\pi}{2} < \theta < \frac{3\pi}{2} \tag{A.3}$$

and

$$\frac{\partial u_1}{\partial r} = -q_0[u_1 - u_0^2(u_0 - 1)], \quad r = 1, -\frac{\pi}{2} < \theta < \frac{\pi}{2}, \tag{A.4}$$

$$u_1 = 0, \quad r = 1, \frac{\pi}{2} < \theta < \frac{3\pi}{2}. \tag{A.5}$$

From symmetry considerations, approximate solutions, within the frame of the Boundary Collocation Method, will be looked for as linear combinations of polar harmonics in the region $0 \leq r < 1$, $0 \leq \theta \leq \pi$ in the form

$$u_0 = \sum_{n=0}^{N-1} a_n r^n \cos n\theta, \quad u_1 = \sum_{n=0}^{N-1} b_n r^n \cos n\theta, \tag{A.6}$$

where N is an arbitrarily chosen positive integer, usually called the number of degrees of freedom, and a_n and b_n are unknown coefficients to be determined. These forms of the solution obviously satisfy exactly the field equation (Laplace’s equation). Using the Boundary Collocation Method to enforce the boundary conditions at a certain number $M (\geq N)$ of known boundary points $(1, \theta_m)$, $m = 0, 1, 2, \dots, M - 1$, one obtains the following two (overdetermined) systems of $2M$ nonlinear algebraic equations in the $2N$ unknowns $a_0, a_1, a_2, \dots, a_{N-1}$ and $b_0, b_1, b_2, \dots, b_{N-1}$:

$$\sum_{n=0}^{N-1} \left(\frac{n}{q_0} + 1\right) a_n \cos n\theta_m = 1, \quad 0 \leq \theta < \frac{\pi}{2}, \tag{A.7}$$

$$\sum_{n=0}^{N-1} a_n \cos n\theta_m = 2, \quad \frac{\pi}{2} < \theta \leq \pi \tag{A.8}$$

and

$$\sum_{n=0}^{N-1} \left(\frac{n}{q_0} + 1\right) b_n \cos n\theta_m = u_{0m}^2(u_{0m} - 1), \quad 0 \leq \theta < \frac{\pi}{2}, \tag{A.9}$$

$$\sum_{n=0}^{N-1} b_n \cos n\theta_m = 0, \quad \frac{\pi}{2} < \theta \leq \pi, \tag{A.10}$$

where $u_{0m} = u_0(1, \theta_m)$ and $m = 0, 1, 2, \dots, M - 1$.

The system (11)–(14) will be solved for different values of N in two stages: First, one solves (11), (12) for

a_n , from which u_0 is calculated. Then, using the obtained function, one solves (13), (14) for b_n , from which u_1 is calculated. For each value of N , the corresponding optimal value of M will be determined for the least error in satisfying the boundary conditions. It is known that the Boundary Collocation Method generally performs effectively and produces highly accurate results. However, the error in satisfying the boundary conditions is not monotonically decreasing with N . Initially, the error decreases up to a certain critical value of N , after which such a behaviour fails to persist and the error increases or oscillates. The error measure is defined as follows:

$$\varepsilon = \sup_{\theta \in [0, \pi]} ER(\theta), \tag{A.11}$$

with

$$ER(\theta) = \begin{cases} |ER1(\theta)|, & 0 \leq \theta < \frac{\pi}{2} \\ |ER2(\theta)|, & \frac{\pi}{2} < \theta \leq \pi \end{cases} \tag{A.12}$$

and

$$ER1(\theta) = \sum_{n=0}^{N-1} \left(\frac{n}{q_0} + 1\right) (a_n + \alpha b_n) \cos n\theta - 1 \tag{A.13}$$

$$- \alpha \left(\sum_{n=0}^{N-1} a_n \cos n\theta\right)^2 \left(\sum_{n=0}^{N-1} a_n \cos n\theta - 1\right), \tag{A.14}$$

$$ER2(\theta) = \sum_{n=0}^{N-1} (a_n + \alpha b_n) \cos n\theta_m - 2. \tag{A.15}$$

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