

Project: Using dolphin whistles to identify species.

Dr P. Dobbins

Ultra Electronics Sonar Systems

Dolphin whistles form time-frequency contours that are complex, overlapping, and unpredictable [1]. These features make automatic detection, classification and localisation of whistles difficult and labour-intensive. However, all such whistles fall within a fixed range of time and frequency parameters [2]. It has previously been demonstrated that a dolphin whistle detector can be constructed in MATLAB using this information [3, 4] and it is hoped to build on the achievements of that project by identifying which of the thirty-three species of marine dolphins produced the whistle. The project will start with a brief literature search for dolphin whistle classification techniques and a review of the theory behind any that are found. Then it will proceed to collect and analyse a set of the previously recorded dolphin whistles available at various internet sites, to extract the time and frequency statistics and then to determine the differences between a limited selection of species. Given this information, the main challenge in this project will be to develop a pattern recognition algorithm which identifies signals that match the specific set of parameters for a particular species, whilst rejecting interference such as ambient noise and transient sounds. This algorithm could be based on the previous MATLAB whistle detector [3], algorithms published in the literature, or could take an entirely new approach. Finally, the probability of detection and false alarm rate of the algorithm will be assessed using a different set of previously recorded whistles.

## References

- [1] Caldwell, M.C. and D.K. Caldwell, 1965. Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus*). *Nature*, 207 434-435.
- [2] Bazúa-Durán, C., 2004. Differences in the whistle characteristics and repertoire of Bottlenose and Spinner Dolphins. *Anais da Academia Brasileira de Ciências*, 76(2) 386-392.
- [3] Hoffmann, Franca, 2014. CCA mini-project report: *Dolphin Whistle Detector Algorithms: A New Robust Dolphin Detector using Coherence Enhanced Diffusion*
- [4] Dobbins, P. and F. Hoffman, A new, robust, dolphin whistle detector algorithm, *Institute of Acoustics 40th Anniversary Conference*, NEC, Birmingham, 15-16 October 2014

## Project Accovion

One of the main challenges in medical research is to demonstrate that a new therapy is at least as good, or possibly better than an already established standard. An example is to show that a generic formulation of a compound is as effective as the original medication. Such a claim is usually based on a clinical trial with hundreds or even thousands of patients in a large number of investigative sites or clinics.

From a statistical perspective, this claim can be confirmed using a test for equivalence or non-inferiority of an experimental treatment compared to the reference treatment. In the frequentist framework commonly used in drug development, this test is based on a shifted null hypothesis of the risk difference.

For single sites trials, the problem has been solved already by Farrington and Manning (1990). If the assumption of a single site trial is not met, methods to combine the data collected in a large number of investigative sites or clinics by means of a valid stratified test are needed. Although Newcombe (1998) developed a confidence interval for the stratified situation a corresponding statistical test has not been available yet.

Accovion GmbH wants to evaluate whether such a corresponding statistical test exists, how this test can be constructed if possible and how it can be implemented in statistical software like R. Both analytical methods as well as heuristic approaches based on simulation or boot-strapping may be employed.

Contact: Mrs. Birgit Keller, Director Biostatistics,  
Email: [birgit.keller@accovion.com](mailto:birgit.keller@accovion.com)

## Literature

Agresti, A. (2013), *Categorical Data Analysis*, 3rd Edition, Hoboken, NJ: John Wiley & Sons.

Farrington, P. and Manning, G. (1990), *Test Statistics and sample size Formulae for comparative binomial trials with null hypothesis of non-zero risk difference or non-unity relative risk*, Statistics in Medicine, 9, 1447-1454

Newcombe, R.G. (1998), *Interval estimation for the difference between independent proportions: Comparison of eleven methods*. Statist. Med. 17, 873-890.

Newcombe, R. G. and Nurminen, M. (2011), *In Defence of Score Intervals for Proportions and Their Differences*, Communications in Statistics—Theory and Methods, 40, 1271–1282

## Joint Modelling of Deformation and Template Maps of Cortical Surface Thickness of Bone

This project will examine how to jointly model surfaces of data taken from scans of human femurs. Interest will be in how shape affects cortical thickness. By combining work based on applying constrained statistical models to surface data with work on applying joint statistical models for signal alignment in 1-D, the aim of the project will be to produce statistical models which can combine information from both the data once available on a template and additionally the warping to put the data on the template in the first place. This will require the combinations of a number of techniques including functional data analysis and finite element methods for surface discretisation, as well as an understanding on the underlying deformation process. The final analysis will be applied to a large data set of femur bones, allowing insight into cortical thickness variation, which has considerable implications in understanding fracture risk.

Jointly supervised by Andrew Gee (Engineering), Graham Treece (Engineering) and John Aston (Statslab).

## Compressed Sensing of Helium Atom Scattering Spectra

Supervisor: Bill Allison, Surfaces, Microstructure and Fracture Group, Cavendish Laboratory

The project would be based on a recent paper titled "Continuous Compressed Sensing of Inelastic and Quasielastic Helium Atom Scattering Spectra"

[http://www.damtp.cam.ac.uk/research/afha/anders/CS4HAS\\_Arxiv\\_2.pdf](http://www.damtp.cam.ac.uk/research/afha/anders/CS4HAS_Arxiv_2.pdf).

Basically, I would implement the Compressed Sensing techniques that are presented in this paper, applied to the study of the dynamical behaviour of surfaces on an atomic level. The computational side would be done on MATLAB.

## Modelling and simulation with PDEs

Supervisor: Prof. Erik von Harbou, Department of Mechanical and Process Engineering, University of Kaiserslautern

The aim of the project that has been proposed by Jun.-Prof. Erik von Harbou (Department of mechanical and process engineering, University of Kaiserslautern) is to model an instationary, isothermal chromatographic fixed-bed reactor. The system of partial differential equations describing this chemical reactor have been proposed in the paper "Quantifying temperature and flow rate effects on the performance of a fixed-bed chromatographic reactor", written by Tien D. Vu and A. Seidel-Morgenstern. The task is to solve this system of PDEs both accurately and efficiently. If time permits, one may also optimise the process with respect to certain criteria.



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# Parental care as a differential game: A dynamic extension of the Houston–Davies game

Christian-Oliver Ewald <sup>a,\*</sup>, John McNamara <sup>b</sup>, Alasdair Houston <sup>c</sup>

<sup>a</sup> Department of Economics, University of St. Andrews, St. Salvator's College, St. Andrews, Fife KY16 9AL, Scotland, UK

<sup>b</sup> Department of Mathematics, University of Bristol, University Walk, Bristol BS8 1TW, UK

<sup>c</sup> School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

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## Abstract

An interpretation of the conflict between male and female parents during the process of caring for their common offspring by means of Game Theory was given in Houston and Davies. [A.I. Houston, N.B. Davies, The evolution of cooperation and life history in the dunnock *Prunella modularis*, in: R.M. Sibly, R.H. Smith (Eds.), Behavioral Ecology, Blackwell Scientific Publications, 1985, pp. 471–487]. Mathematically, this model represents a static game with continuous strategy sets. Recently, this model was reconsidered in a dynamic discrete time framework which also included state dependencies [J.M. McNamara et al., A dynamic game-theoretic model of parental care, *J. Theor. Biol.* 205 (2000) 605–623]. In this article, we give an interpretation of the parental care conflict in continuous time by means of a differential game with state dependent strategies.

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## 1. Introduction

The parental care conflict between the male and female parent about who provides which level of effort during the time when care for the offspring is necessary presents a well-known example in theoretical biology, where game theory can be applied very successfully, see [1,3,9] as only to mention a few examples. For a general review of this topic, we refer to the article [5]. Two features which were neglected in the early models, were time-dependent dynamic strategies as well as state dependency. McNamara et al. [8] introduced a model which included these two features and lead to interesting results which could not have been obtained with the static models studied before. This model is mostly based on discrete time techniques. In the current paper, we give an alternative interpretation of the parental care conflict in terms of a differential game, which is based on time-dependent strategies, includes the feature of state dependency and leads to analytically tractable results.

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\* Corresponding author.

E-mail address: [ce16@st-andrews.ac.uk](mailto:ce16@st-andrews.ac.uk) (C.-O. Ewald).

It also has the nice property that the original static Houston–Davies game from [4] can be naturally embedded in this game. The main solution technique for differential games is an adaptation of the Hamilton–Jacobi–Bellman equation, which translates the problem of finding the evolutionary stable strategy (ESS) into the problem of solving a particular PDE. Differential games have been applied very successfully in economics and one can find numerous examples of such games in the economic literature, see for example [2] for many references. The structure of the parental care game discussed in this article has to the best of our knowledge not been studied before. It is not zero-sum and not of the linear-quadratic type and simple separation of variable approaches fail. In order to solve the Hamilton–Jacobi–Bellman equation arising from our parental care game we apply the technique of characteristic equations, see [6]. This technique translates our partial differential equation into a system of ordinary differential equations, which are easier to solve. The solutions of these ordinary differential equations lead to certain curves in space time along which the PDE can be solved. We find that along these curves the ESS's and the value function are represented by very simple expressions. This assigns a biologically fundamental meaning to these curves. The article is organized as follows. We review the static Houston–Davies game in Section 2. This game presents the parental care conflict in its simplest form and since its introduction has served as a benchmark example. In Section 3, we consider symmetric differential games and their equilibrium concepts as well as existence results based on the so-called Hamilton–Jacobi–Bellman equation, while in Section 4 we study the method of characteristic curves, which allows us to solve the Hamilton–Jacobi–Bellman equation in cases where simple separation of variable arguments fail. Our differential game version of the parental care conflict is presented in Section 5 and useful results for the structure of the ESS are derived for the general form. Furthermore, we provide a concrete example, where we give explicit and analytic formulas for the ESS as well as certain related functionals. In Section 6, we extend the model from Section 5, by adding energy-levels of each parent to the state process and introducing feedback strategies which depend not only on the offspring welfare, but also on the energy-levels. We show however, that by using such strategies, parents cannot do better, and that the ESS for this game is in fact independent of energy levels. We compare the newly obtained dynamic ESS with the static ESS for the Houston–Davies game in Section 7 by using a natural embedding of the static Houston–Davies game into our class of dynamic differential games. Furthermore we study certain other aspects such as the well being of the offspring under different scenarios of parents choice of strategy. We summarize the main conclusions in Section 8.

## 2. The static Houston–Davies parental care game

Let us consider the following parental care game, which was introduced in [4] and along with [7] represents one of the first game theoretic models of the parental care conflict. All members of a given sex are assumed to be identical and in order to simplify our arguments and be in line with the discussion which is to follow after this section we also assume that there are no qualitative differences between the two sexes. At the beginning of the breeding process each parent makes a single choice of effort  $\phi_1$  resp.  $\phi_2 \in [0, \infty)$ , not knowing the others choice. If the male provides effort  $\phi_1$  and the female provides effort  $\phi_2$  then  $B(\phi_1 + \phi_2)$  measures the present reproductive success. Here,  $B : [0, \infty) \rightarrow \mathbb{R}_+$  is a function which we assume is two times continuously differentiable and satisfies  $B'(x) > 0$  and  $B''(x) < 0$  for all  $x \in [0, \infty)$ , i.e.  $B(\cdot)$  is strictly increasing and strictly concave. This is a realistic assumption.  $B(\phi_1 + \phi_2)$  can be interpreted as the expected number of offspring in the current brood surviving to maturity or alternatively, the aggregate level of fitness of the offspring. Increasing effort should increase the chances of survival and the fitness of the offspring, whereas the effectiveness in increasing the survival chances decreases with the level of care given. Investing effort into the care process leads to individual costs for the male resp. female which in return leads to a decrease of future reproductive success. These costs are incorporated into the model by a cost function  $C : [0, \infty) \rightarrow \mathbb{R}_+$  where  $C(\phi_1)$  resp.  $C(\phi_2)$  indicate the costs for a male caring with effort  $\phi_1$  resp. a female caring with effort  $\phi_2$ . As indicated before, in order to remain in a symmetric game framework we assume that male and female share the same cost function. We assume that  $C(\cdot)$  is two times continuously differentiable and satisfies  $C'(x) > 0$  and  $C''(x) > 0$  for all  $x \in [0, \infty)$ , i.e.  $C(\cdot)$  is strictly increasing and strictly convex. The total reproductive success in this model, i.e. the sum of reproductive success from the present offspring and future reproductive success, is then given by  $B(\phi_1 + \phi_2) - C(\phi_1)$  for the male and  $B(\phi_1 + \phi_2) - C(\phi_2)$  for the female, given that the male effort is  $\phi_1$  and the female effort is  $\phi_2$ . Taking  $\mathcal{S}_i = [0, \infty)$  for  $i = 1, 2$  as the set of pure strategies and defining the payoffs as

$$\begin{aligned}\pi_1(\phi_1, \phi_2) &= B(\phi_1 + \phi_2) - C(\phi_1), \\ \pi_2(\phi_1, \phi_2) &= B(\phi_1 + \phi_2) - C(\phi_2),\end{aligned}$$

we obtain a symmetric two player game with continuous pure strategy sets. A symmetric Nash-equilibrium  $\Phi^*$  for this game has to satisfy the condition

$$\phi^* = \arg \max_{\phi \in [0, \infty)} \pi_1(\phi, \phi^*)$$

which given our assumption on the function  $B$  and  $C$  is implied by  $\frac{\partial}{\partial \phi} \pi_1(\phi, \phi^*)|_{\phi=\phi^*} = 0$ . This is equivalent to  $B'(2\phi^*) = C'(\phi^*)$ . (1)

Any solution of Eq. (1) leads to a symmetric Nash-equilibrium. If in fact the solution is unique, it can easily be verified that the corresponding Nash-equilibrium is also an ESS. Let us consider the following choices for  $B(\cdot)$  and  $C(\cdot)$ , which we will later compare to the dynamic differential game framework:  $B(\phi) = \ln(T \cdot \phi + 1)$  and  $C(\phi) = \frac{kT}{2} \phi^2$ . The parameter  $T > 0$  represents the length of the caring process, while  $k$  represents a cost factor. With these choices Eq. (1) translates into  $\frac{T}{2\phi^* T + 1} = \phi^* T \cdot k$ . This equation has exactly one positive solution  $\phi^*$ , which is given by

$$\phi^* = \frac{\sqrt{1 + \frac{8T}{k}} - 1}{4T}. \quad (2)$$

The strategy  $\phi^*$  is therefore an ESS in the static Houston–Davies game described above. We will later demonstrate how the static Houston–Davies game can be embedded in our dynamic differential game framework and compare the performance of  $\phi^*$  with the ESS for the corresponding differential game as well as the effects on the offspring.

### 3. A brief review on symmetric differential games

Before we start extending the static parental care game discussed in the previous section into a dynamic differential game let us now briefly review the subject of differential games. We concentrate on feedback strategies which depend on time and the current state of the system and allow the players to make their decision dependent on the dynamic state of the underlying model. We do not discuss open loop strategies which only depend on the initial state of the system and which we consider as to static. The main non-cooperative solution concept for differential games with feedback strategies is that of a feedback Nash-equilibrium which we discuss later in this section. The computation of such feedback Nash-equilibria is based on an extension of the well-known Hamilton–Jacobi–Bellman equation from classical optimal control theory. For a thorough treatment of differential games see [2]. An excellent overview of the main results can also be found in the second chapter of [10]. In this article, we only consider a symmetric two player framework and therefore restrict our discussion on the case of symmetric feedback Nash-equilibria. This simplifies the in general rather technical discussion of the existence and characterization of feedback Nash-equilibria considerably, as it allows us to avoid systems of partial differential equations and work with one single partial differential equation instead. Given these assumptions the players in such a differential game use strategies of the type  $\varphi(s, x)$  which depend on time  $s$  and the state  $x \in \mathbb{R}^m$  of the system at time  $s$ . These strategies in fact control the state of the system in the way that the state dynamics is given by a controlled differential equation

$$\dot{X}(s) = f(s, X(s), \varphi_1(s, X(s)), \varphi_2(s, X(s))). \quad (3)$$

Note that we denote the state trajectory with a capital letter  $X$  in order to distinguish it from the state variable  $x$  and the later occurring characteristic curve, which will be denoted by  $x(\cdot)$ . In order to remain in a really symmetric framework, we have to assume that the function  $f$  is symmetric in the third and fourth argument, i.e.  $f(s, x, y_1, y_2) = f(s, x, y_2, y_1)$ . This assumption represents the idea that the growth-rate of the state of the system depends only on the two strategies which are used, but not on which player is using which strategy. In many cases, this represents a reasonable assumption. Strategies are assumed to be admissible, which means that given a pair of strategies  $\varphi_1(s, x), \varphi_2(s, x)$  the ODE (3) has a unique solution. Whenever we speak of

strategies in the following, we mean admissible strategies. Both players then use strategies in order to maximize their payoffs which are assumed to be of the following type

$$J^i = \int_0^T F(s, X(s), \varphi_i(s, X(s)), \varphi_{-i}(s, X(s))) ds + q(X(T)) \quad (4)$$

for  $i = 1, 2$ , where  $F(s, x, y_1, y_2)$  and  $q(x)$  are sufficiently smooth functions. Here, we use the standard notation, that  $-i$  denotes the complementary index. The following definition presents the concept of a symmetric feedback Nash-equilibrium.

**Definition 3.1.** A symmetric feedback Nash-equilibrium strategy for the two player symmetric differential game presented above is a feedback strategy  $\varphi^*(s, x)$  for which there exists a function  $V(t, x)$ , defined on  $[0, T] \times \mathbb{R}^m$  s.t.  $V(T, x) = q(x)$  and

$$\begin{aligned} V(t, x) &= \int_t^T F(s, X^*(s), \varphi^*(s, X^*(s)), \varphi^*(s, X^*(s))) ds + q(X^*(T)) \\ &\geq \int_t^T F(s, X(s), \varphi(s, X(s)), \varphi^*(s, X(s))) ds + q(X(T)) \end{aligned}$$

for all feedback strategies  $\varphi(s, x)$ ,  $x \in \mathbb{R}^m$  and  $t \in [0, T]$ . Here,  $X^*(s)$  resp.  $X(s)$  denote the trajectories of the state variable given the strategy pairs  $(\varphi^*(s, x), \varphi^*(s, x))$  resp.  $(\varphi(s, x), \varphi^*(s, x))$  and initial condition  $x^*(t) = x(t) = x$ .

The function  $V(t, x)$  is called the value function. One important feature of the equilibrium concept defined above, is that if a strategy provides a feedback Nash-equilibria and one restricts the game to a sub-game starting at time  $t \in [0, T]$  and some initial state  $x \in \mathbb{R}^m$  at time  $t$ , then the same strategy defines a feedback Nash-equilibrium for that sub-game as well. In a classical game theoretic framework we would call such a strategy a sub-game perfect Nash-equilibria. Let us now come to the main tool which helps us to compute feedback Nash-equilibria. It is based on a suitable adaptation of the classical Hamilton–Jacobi–Bellman equation for standard optimal control problems.

**Proposition 3.1.** *A feedback strategy  $\varphi^*(s, x)$  provides a symmetric feedback Nash-equilibrium for the differential game introduced above, if there exist a continuously differentiable function  $V(t, x) : [0, T] \times \mathbb{R}^m \rightarrow \mathbb{R}$  satisfying the following partial differential equations:  $V(T, x) = q(x)$  and*

$$\begin{aligned} -V_t(t, x) &= \max_u \{F(t, x, u, \varphi^*(t, x)) + V_x(t, x)f(t, x, u, \varphi^*(t, x))\} \\ &= F(t, x, \varphi^*(t, x), \varphi^*(t, x)) + V_x(t, x)f(t, x, \varphi^*(t, x), \varphi^*(t, x)), \end{aligned}$$

where the maximization above is over all admissible controls at time  $t$  and state  $x$ .

**Proof.** This follows easily from Theorem 2.2.3 in [10, p. 28].  $\square$

In the following, we will illustrate how to apply this proposition in practice. The discussion is very informal and we leave out the technical details. Assume we are carrying out the maximization above point-wise in  $u$ . A necessary condition for  $\varphi^*(t, x)$  to be the maximizer would then be that

$$\frac{\partial}{\partial u} F(t, x, u, \varphi^*(t, x))|_{u=\varphi^*(t, x)} + V_x(t, x) \frac{\partial}{\partial u} \cdot f(t, x, u, \varphi^*(t, x))|_{u=\varphi^*(t, x)} = 0.$$

Assume for simplicity that a unique solution  $\varphi^*(t, x)$  of this equation exists and that it indeed represents the maximizer. This solution can be written as  $\varphi^*(t, x) = h(t, x, V_x(t, x))$  with a function  $h(t, x, p)$ . The latter function can be substituted for the maximizer in the maximization above and this leads to an equation of the form

$$0 = H(t, x, V_x(t, x)) + V_t(t, x) \quad (5)$$

with another function  $H(t, x, p)$ . Eq. (5) represents a non-linear first-order partial differential equation which can be dealt with, by methods from partial differential equations. In the following section demonstrate how to solve this type of PDE.

#### 4. The method of characteristics

Let us consider a first-order but possibly non-linear partial differential equation of the following type

$$H(t, x, u_x(t, x)) + u_t(t, x) = 0$$

with initial condition  $u_0(0, x) = u_0(x)$ , where  $H(t, x, p)$  is a continuously differentiable function. Such equations are generally referred to as Hamilton–Jacobi equations. While we will not make use of any general existence result for solutions of PDE's of this type, basically because we construct solutions in the individual cases which are of interest for us, it is important to note that if  $H(t, x, p)$  satisfies a local Lipschitz condition in the variable  $p$ , then a solution is unique, see Theorem 1, [6, p. 77]. Sometimes it is possible to derive closed form solutions by use of a simple separation of variable approach, which leads to a system of ordinary differential equations which are easier to solve. In fact, in most examples seen in the economic and management literature this is the case. In our differential version of the parental care game, this technique however does not work. We therefore illustrate an advanced technique how to solve Hamilton–Jacobi equations, which is known as the method of characteristic functions. The idea is, similar to the separation of variables approach, to reduce the PDE into a system of ordinary differential equations. However, instead of separating the two autonomous variables  $t$  and  $x$  the space will be partitioned into one-dimensional curves of the form  $\{(t, x^\xi(t)) | t \in [0, \eta(\xi)]\}$ , where now  $x^\xi(t)$  is assumed to be a function of time, and the PDE is solved along these curves. We assume that  $x^\xi(0) = \xi \in \mathbb{R}$  and that the set of curves is parameterized in this way by  $\xi$ . We will later specify these curves in terms of ordinary differential equations. For now assume that one curve for one particular  $\xi$  has been picked and to simplify notation omit  $\xi$  in the notation. Let us also assume that the curves are continuously differentiable and denote with  $\dot{x}(t)$  the time derivative of  $x(t)$ . Finally assume that a sufficiently smooth solution  $u(t, x)$  of the PDE above exists. Denote with  $v(t)$  the function  $v(t) := u(t, x(t))$ . This function represents the restriction of the function  $u$  to the one dimensional curve identified by  $x(\cdot)$ . Let us furthermore define functions  $p(t) = u_x(t, x(t))$  and  $q(t) = u_t(t, x(t))$ , where  $u_x(t, x)$  and  $u_t(t, x)$  denote the partial derivatives of the function  $u(t, x)$  with respect to  $x$  and  $t$ . The derivative of  $v(\cdot)$  with respect to time can now be computed as

$$\dot{v}(t) = u_t(t, x(t)) + u_x(t, x(t)) \cdot \dot{x}(t) = q(t) + p(t) \cdot \dot{x}(t).$$

For the time derivative of  $p(\cdot)$  and  $q(\cdot)$  we compute

$$\dot{p}(t) = u_{xt}(t, x(t)) + u_{xx}(t, x(t)) \cdot \dot{x}(t), \quad (6)$$

$$\dot{q}(t) = u_{tt}(t, x(t)) + u_{tx}(t, x(t)) \cdot \dot{x}(t). \quad (7)$$

On the other side, by differentiating the original PDE for  $u(t, x)$  with respect to  $x$  resp.  $t$  we obtain

$$H_x(t, x, u_x(t, x)) + H_p(t, x, u_x(t, x)) \cdot u_{xx}(t, x) + u_{tx}(t, x) = 0, \quad (8)$$

$$H_t(t, x, u_x(t, x)) + H_p(t, x, u_x(t, x)) \cdot u_{xt}(t, x) + u_{tt}(t, x) = 0. \quad (9)$$

If we now specify  $x(t)$  as the solution of the ordinary differential equation

$$\dot{x}(t) = H_p(t, x(t), u_x(t, x(t))), \quad x(0) = \xi, \quad (10)$$

where  $\xi$  is the parameter discussed in the beginning of this section, we can, by using Eqs. (8) and (9), write Eqs. (6) and (7) as follows:

$$\dot{p}(t) = -H_x(t, x(t), p(t)), \quad (11)$$

$$\dot{q}(t) = -H_t(t, x(t), p(t)). \quad (12)$$

Furthermore, we obtain for the time derivative of  $v(\cdot)$  the equation

$$\dot{v}(t) = q(t) + p(t) \cdot H_p(t, x(t), p(t)), \quad v(0) = u(0, x(0)) = u_0(\xi). \quad (13)$$

The values for  $p(0)$  and  $q(0)$  are identified as follows:

$$p(0) = u_x(0, x(0)) = \frac{\partial}{\partial x} u_0(x)_{x=\xi} = u'_0(\xi) \quad (14)$$

while  $q(0)$  can be obtained from

$$0 = H(0, \xi, u'_0(\xi)) + q(0) \iff q(0) = -H(0, \xi, u'_0(\xi)). \quad (15)$$

Eqs. (10)–(13) together with the corresponding initial conditions represent a system of four ordinary differential equations for the functions  $x(\cdot), p(\cdot), q(\cdot)$  and  $v(\cdot)$ . Let us remind that all these functions depend implicitly on the parameter  $\xi$  which was chosen to be the initial value of the function  $x(\cdot)$ . In order to compute the value of the function  $u(t, x)$  at a particular point  $(t, x)$  one can now try to determine  $\xi = \xi(t, x)$  as a function of  $t$  and  $x$  in a way that  $x^\xi(t) = x$ . If this is possible we have  $u(t, x) = v^{\xi(t,x)}(t)$ .

## 5. A differential parental care game and its feedback Nash-equilibria

In this section, we present our dynamic differential game model for the parental care conflict in continuous time. The framework is that of symmetric differential games with feedback strategies as discussed in the previous section. For this purpose, we define the state variable  $X(t) = \text{Level of fitness of offspring at time } t$ . We assume that the benefit for the parents is determined by the variable  $x(T)$ , where  $T$  denotes the end of the care period. In the following, we assume that there are no major asymmetries between male and female and that the benefit for male and female is the same. The actions for male and female are given by choosing an instantaneous level of effort at time  $t$ . As indicated before, we assume that the information level of male and female is accurately given by using feedback strategies of the form  $\varphi_i(s, x) = \text{Level of instantaneous effort given times and state } x$ . Here,  $\varphi_1(s, x)$  denotes the level for the male and  $\varphi_2(s, x)$  the level of the female, respectively. The costs  $C_i(t)$  accumulated up to time  $t$  caused by such a strategy are assumed to be given by

$$C_i(t) = \frac{k}{2} \int_0^t \varphi_i(s, X(s))^2 ds, \quad i = 1, 2, \quad (16)$$

where  $k$  represents a cost factor. The payoffs for male and female are then given by the difference of benefit and costs, i.e.

$$J^i := X(T) - C_i(T). \quad (17)$$

By looking at this payoff function one might be tempted to say that there is no decreasing marginal benefits, because the state variable  $X(T)$  enters linearly. This however is not correct. The decreasing marginal benefits from effort levels are incorporated in the controlled differential equation for the state variable  $X(t)$ . Here, we assume that  $X(t)$  is given by the following differential equation

$$\dot{X}(t) = b(X(t), \varphi_1(t, X(t)) + \varphi_2(t, X(t))) \quad (18)$$

with the initial condition  $X(0) = 0$ . The function  $b(x, y)$  controls the growth rate of the offspring's fitness level. We will assume that this growth rate is always positive, meaning that over the caring period the offspring cannot loose any fitness, even though the parents may radically decrease their effort levels. We assume in the following that the growth rate function  $b(x, y)$  is of the type

$$b(x, y) = y \cdot g(x), \quad (19)$$

where  $g$  is a function which we specify later. Looking at Eq. (19) we see that the sum of the two effort levels of the parents has a linear effect on the instantaneous growth rate and that the state dependency of the growth rate is modeled by the function  $g(x)$ . From a biological point of view, we think of the function  $g(x)$  as a metabolic factor, which measures the effect an absolute effort of  $y$  has on the offspring's fitness, given the offspring's current state is equal to  $x$ . It is precisely this function  $g(x)$  which we use in order to model the effect of decreasing marginal benefits from effort levels. Let us illustrate this in the following. First note that the static Houston–Davies model is embedded in our dynamic framework by choosing the strategies  $\varphi_i(s, x)$  of male and female to be state independent and constant in time, i.e.  $\varphi_i(s, x) \equiv \phi_i$  with  $\phi_i \in \mathbb{R}$ . By choosing such strategies the differential equation for the state variable  $X(t)$  becomes  $\dot{X}(t) = (\phi_1 + \phi_2) \cdot g(x(t))$ . By setting  $y = \phi_1 + \phi_2$  and denoting the dependence of the solution of the differential equation above on  $y$  by a subindex we obtain the differential equation:

$$\dot{X}_y(t) = y \cdot g(X_y(t)), \quad X_y(0) = 0. \quad (20)$$

The chosen model then accurately represents the effect of decreasing marginal benefits to effort levels if the function  $B(y) := X_y(T)$  is increasing and concave. We assume in the following that this is the case. On the

other side, the following lemma shows how to re-obtain a given static benefit function  $B(\cdot)$  as in Section 2, by choosing a specific function  $g(\cdot)$ .

**Lemma 5.1.** *Let  $B(\cdot)$  be a strictly concave or strictly convex continuously differentiable function with  $B(0) = 0$ . Define the function  $g(x) := \frac{1}{T} \cdot \frac{1}{(B^{-1})'(x)}$ , where  $B^{-1}(\cdot)$  denotes the inverse function of  $B(\cdot)$ . Then the solution  $X_y(t)$  of the differential equation (20) satisfies  $X_y(T) = B(y)$ .*

**Proof.** We have

$$\begin{aligned}\frac{d}{dt}(B^{-1}(X_y(t))) &= (B^{-1})'(X_y(t)) \cdot \dot{X}_y(t) = (B^{-1})'(X_y(t)) \cdot y \cdot g(X_y(t)) \\ &= (B^{-1})'(X_y(t)) \cdot y \cdot \frac{1}{T} \frac{1}{(B^{-1})'(X_y(t))} = \frac{y}{T}\end{aligned}$$

Integration over  $[0, T]$  gives  $B^{-1}(X_y(T)) = y$  and therefore  $X_y(T) = B(y)$ , which was to prove.  $\square$

We also observe that static strategies, when substituted in the dynamic cost functional in Eq. (16), lead to static quadratic costs. The situation is completely similar when the quadratic instantaneous costs are substituted by some other cost functional. We therefore conclude from Lemma 5.1 that the static Houston–Davies framework can be completely embedded in the dynamic differential game framework presented in this section. Our main example leading to logarithmic static utility is obtained by choosing  $g(x) = e^{-x}$  which leads to  $B(z) = \ln(Tz + 1)$  as in example discussed in Section 2. We will later discuss this case explicitly.

Let us now try to solve the differential game discussed above for symmetric feedback Nash-equilibria. As already indicated in Section 3, we are mainly interested in symmetric Nash-equilibria since they are more meaningful from an evolutionary point of view and from the symmetries apparent in our model. In order to do this let us set up the Hamilton–Jacobi–Bellman equation for this problem. The functions  $F$ ,  $q$  and  $f$  in the setup of Section 4 are given, respectively, by  $F(s, x, y_1, y_2) = -\frac{k}{2}y_1^2$ ,  $q(x) = x$  and  $f(s, x, y_1, y_2) = b(x, y_1 + y_2)$ . Let  $V(t, x)$  denote the value function for either male or female, as discussed in Section 3. For a feedback symmetric Nash-equilibrium  $\varphi^*(s, x)$  this functions would have to satisfy the following equations:  $V(T, x) = x$  and

$$\begin{aligned}-V_t(t, x) &= \max_u \left\{ -\frac{k}{2}u^2 + V_x(t, x) \cdot b(x, u + \varphi^*(t, x)) \right\}, \\ &= -\frac{k}{2}\varphi^*(t, x)^2 + V_x(t, x) \cdot b(x, 2\varphi^*(t, x)).\end{aligned}$$

Let us compute the maximizer  $u(t, x) = \varphi^*(t, x)$  in the equation above. Differentiating and setting the result equal to zero leads to the following equation:

$$-k \cdot \varphi^*(t, x) + V_x(t, x) \cdot \frac{\partial}{\partial y} b(x, 2\varphi^*(t, x)) = 0.$$

It follows from our assumption  $b(x, y) = y \cdot g(x)$  that  $\frac{\partial}{\partial y} b(x, y) = g(x)$ . Substituting this in the equation above and solving for  $\varphi^*(t, x)$  leads to

$$\varphi^*(t, x) = \frac{1}{k}V_x(t, x) \cdot g(x).$$

We now substitute this expression in the original Hamilton–Jacobi–Bellman equation and obtain

$$-V_t(t, x) = -\frac{1}{2k}V_x(t, x)^2 \cdot g(x)^2 + V_x(t, x) \cdot \frac{2}{k} \cdot V_x(t, x) \cdot g(x) \cdot g(x) = \frac{3}{2k}V_x(t, x)^2 \cdot g(x)^2.$$

The following result is therefore a direct consequence of Proposition 3.1.

**Proposition 5.1.** *If the following non-linear first-order boundary value problem*

$$-V_t(t, x) = \frac{3}{2k}V_x(t, x)^2 \cdot g(x)^2, \quad V(T, x) = x \tag{21}$$

has a solution, then a symmetric feedback Nash-equilibrium strategy  $\varphi^*(t, x)$  for the differential parental care game exists and is given by the equation

$$\varphi^*(t, x) = \frac{1}{k} V_x(t, x) \cdot g(x). \quad (22)$$

We note that uniqueness of a possible solution of PDE (21) is guaranteed by Theorem 1, in [6, p. 77]. Let us now use the method of characteristic functions explained in the previous section to transform the problem of solving the PDE (21) in Proposition 5.1 into a problem concerning ordinary differential equation. The following proposition is a key result as it gives simple explicit expressions for the value function and the ESS along the characteristic curve.

**Proposition 5.2.** Define  $x(\cdot)$  as the solution of the ordinary differential equation

$$\dot{x}(t) = -\frac{3}{k} g(\xi) g(x(t)), \quad x(0) = \xi \in \mathbb{R}. \quad (23)$$

Then the solution  $V(t, x)$  of (21) satisfies

$$V(T - t, x(t)) = -\frac{3}{2k} g(\xi)^2 t + \xi \quad (24)$$

for  $t \in [0, T]$  and the ESS is constant along the curve with values

$$\varphi^*(T - t, x(t)) = \frac{1}{k} g(\xi). \quad (25)$$

Let us discuss this result, before we continue with its proof. The value function and even more the strategy appear to have a very simple form. This form however could only be obtained after changing the geometry and considering the space-time along the time reversed characteristic curves. The fact that the value function is linear along these curves and the ESS constant however is very striking and might indeed be very useful, when discussing evolutionary dynamics for our differential game.

**Proof.** As indicated before, we will use the theory of characteristic equations in order to prove Proposition 5.2. First of all note that (21) represents a terminal value problem rather than an initial value problem. In order to apply the method of characteristic equations discussed in the last section, we therefore have to perform a time inversion. In order to do this, simply define the function  $u(t, x)$  as  $u(t, x) = V(T - t, x)$ . Using that  $u_t(t, x) = -V_t(T - t, x)$  and  $u_x(t, x) = V_x(T - t, x)$  we find that the PDE for  $V(t, x)$  translates into the following PDE

$$u_t(t, x) = c \cdot u_x(t, x)^2 \cdot g(x)^2, \quad u(0, x) = x$$

with  $c = \frac{3}{2k}$ . In this case, the function  $H$  from the previous section is given by  $H(t, x, p) = -c \cdot p^2 \cdot g(x)^2$ . Noticing that  $H_t \equiv 0$  we derive the characteristic equations for the functions  $x(\cdot)$ ,  $p(\cdot)$  and  $q(\cdot)$  as follows:

$$\dot{x}(t) = -2cp(t) \cdot g(x(t))^2, \quad x(0) = \xi, \quad (26)$$

$$\dot{p}(t) = 2c \cdot p(t)^2 \cdot g(x(t)) \cdot g'(x(t)), \quad p(0) = 1 \quad (27)$$

$$\dot{q}(t) \equiv 0, \quad q(0) = cg(\xi)^2. \quad (28)$$

We see from the last equation, that the function  $q(\cdot)$  must be constant in time and therefore  $q(t) = cg(\xi)^2$  for all  $t$ . The equation for  $v(t) = u(t, x(t))$  is then given by

$$\dot{v}(t) = -2cp(t)^2 \cdot g(x(t))^2 + cg(\xi)^2$$

with  $v(0) = \xi$  and can be obtained by simple integration, once the solutions for  $x(\cdot)$  and  $p(\cdot)$  are known. The main problem is therefore to solve the system of ordinary differential equations (26) and (27). In order to do this let us first observe that (26) and (27) are equivalent to

$$\dot{x}(t) = -2cp(t) \cdot g(x(t))^2, \quad (29)$$

$$\dot{p}(t) = -p(t) \cdot \dot{x}(t) \cdot \frac{g'(x(t))}{g(x(t))} \quad (30)$$

with the corresponding initial conditions. From the chain rule of calculus we have

$$\dot{x}(t) \cdot \frac{g'(x(t))}{g(x(t))} = \frac{d}{dt} \ln(g(x(t)))$$

and therefore that (30) is equivalent to

$$\frac{d}{dt} \ln(p(t)) = \frac{\dot{p}(t)}{p(t)} = -\frac{d}{dt} \ln(g(x(t))) = \frac{d}{dt} \ln\left(\frac{1}{g(x(t))}\right).$$

Integration of this equation leads to  $\ln(p(t)) = \ln\left(\frac{1}{g(x(t))}\right) + \epsilon$  where  $\epsilon$  represents an integration constant. This constant can be easily determined from the initial conditions  $p(0) = 1$  and  $x(0) = \xi$ , and in fact  $\epsilon = \ln(g(\xi))$ . We therefore obtain

$$\ln(p(t)) = \ln\left(\frac{1}{g(x(t))}\right) + \ln(g(\xi)) = \ln\left(\frac{g(\xi)}{g(x(t))}\right)$$

and from this we conclude the useful relationship

$$p(t) = \frac{g(\xi)}{g(x(t))}. \quad (31)$$

Substituting (31) into (29) gives

$$\dot{x}(t) = -2c \frac{g(\xi)}{g(x(t))} \cdot g(x(t))^2 = -2cg(\xi) \cdot g(x(t)).$$

We therefore have transformed the problem into solving the ordinary differential equation

$$\dot{x}(t) = -2cg(\xi) \cdot g(x(t)), \quad x(0) = \xi. \quad (32)$$

This is precisely Eq. (23) and from the general theory of characteristic equations as discussed in Section 4 it follows that

$$\dot{v}(t) = -2c \left( \frac{g(\xi)}{g(x(t))} \right)^2 \cdot g(x(t))^2 + cg(\xi)^2 = -cg(\xi)^2.$$

With  $v(0) = \xi$  it follows immediately that  $v(t) = -cg(\xi)^2 t + \xi$  and therefore

$$V(T-t, x(t)) = u(t, x(t)) = v(t) = -cg(\xi)^2 t + \xi.$$

For the ESS we conclude from Proposition 5.1 that

$$\varphi^*(T-t, x(t)) = \frac{1}{k} V_x(T-t, x(t)) \cdot g(x(t)) = \frac{1}{k} u_x(t, x(t)) \cdot g(x(t)).$$

By definition of the function  $p(\cdot)$  in Section 4 we have  $p(t) = u_x(t, x(t))$  and we therefore conclude from Eq. (31) above that

$$\varphi^*(T-t, x(t)) = \frac{1}{k} \frac{g(\xi)}{g(x(t))} \cdot g(x(t)) = \frac{1}{k} g(\xi)$$

which finishes the proof.  $\square$

In order to give an explicit expression for the function  $V(t, x)$  as a function in the autonomous variable  $t$  and  $x$ , the parameter  $\xi$  has to be determined as a function of  $t$  and  $x$  as indicated in Section 4. We have to notice however, that unless the function  $g(\cdot)$  is not further specified, there is no general way to do this, as Eq. (20) represents more or less a one-dimensional differential equation in its general form. In order to demonstrate how this conversion from  $\xi$  to the variables  $t$  and  $x$  works, we reconsider again the example where the function  $g$  is given by  $g(x) = e^{-x}$ .

**Example 5.1.** Assume  $g(x) = e^{-x}$  and set  $c = \frac{3}{2k}$ . In this case, the ODE for the characteristic curve  $x(\cdot)$  is given by  $\dot{x}(s) = -2ce^{-\xi}e^{-x(s)}, x(0) = \xi$  which leads to  $x^\xi(s) = \ln(-2ce^{-\xi} \cdot s + e^\xi)$ . This equation can be solved for  $\xi$  in

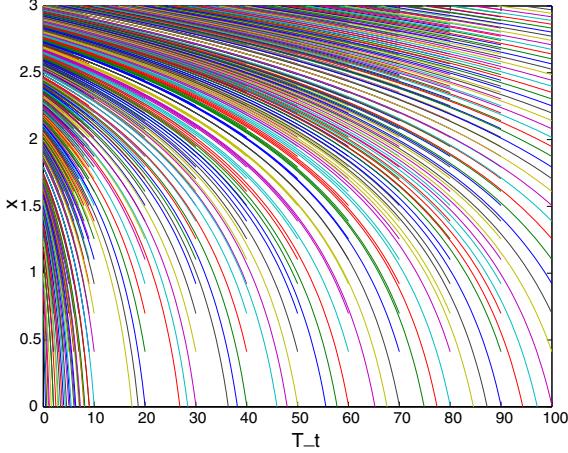


Fig. 1. Characteristic curves.

order to obtain  $x^\xi(t) = x$  with  $\xi(t, x) = \ln(\frac{1}{2}e^x + \frac{1}{2}\sqrt{e^{2x} + 8ct})$ . Please note that there is a singularity in the equation for  $x^\xi(s)$  but that it is well defined for  $s \in [0, t]$  when choosing  $\xi = \xi(t, x)$  as above. The actual characteristic curves are time reversed. The following figure presents an illustration of characteristic curves (see Fig. 1).

Please note that in principal every point in the plane above is finally reach as the endpoint of a characteristic curve, but that for obvious reasons we could not draw all characteristic curves. Substituting the expression from above for  $\xi$  in the corresponding equations for  $V$  and  $\varphi^*$  in (24) and (25) gives

$$V(t, x) = -c \frac{1}{\left(\frac{1}{2}e^x + \frac{1}{2}\sqrt{e^{2x} + 8c(T-t)}\right)^2} \cdot (T-t) + \ln\left(\frac{1}{2}e^x + \frac{1}{2}\sqrt{e^{2x} + 8c(T-t)}\right)$$

as well as

$$\varphi^*(t, x) = \frac{1}{k} \frac{1}{\left(\frac{1}{2}e^x + \frac{1}{2}\sqrt{e^{2x} + 8c(T-t)}\right)}.$$

The dynamics of the offspring fitness under the ESS's is obtained by substituting the expressions from the previous equation into the state dynamic (18):

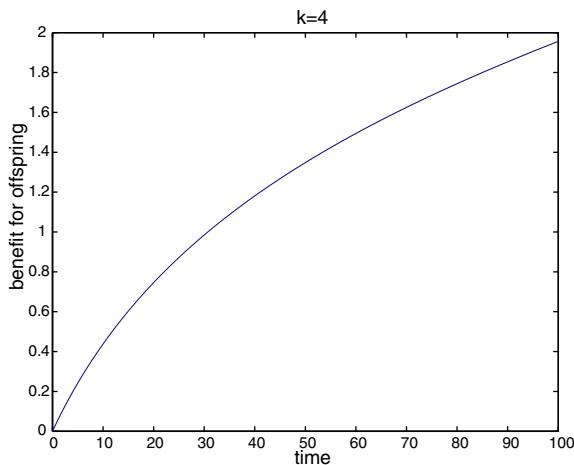
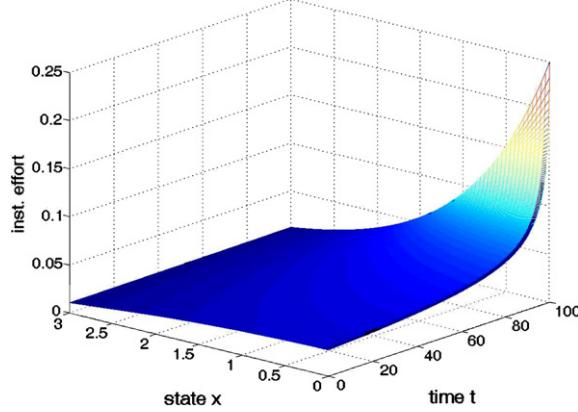
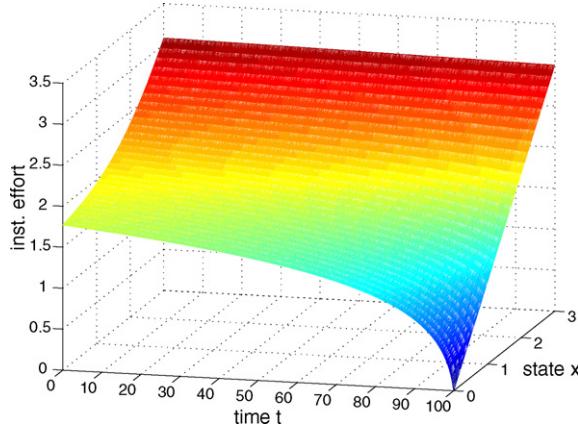


Fig. 2. Dynamics of offspring fitness under ESS.

Fig. 3. Evolutionary strategy,  $k = 4$ ,  $T = 100$ .Fig. 4. Evolutionary strategy,  $k = 4$ ,  $T = 100$ .

$$\dot{X}(t) = \frac{1}{k} \frac{4e^{-X(t)}}{e^{X(t)} + \sqrt{e^{2X(t)} + \frac{12}{k}(T-t)}} \quad (33)$$

with  $X(0) = 0$ . Unfortunately, we were not able to obtain a closed form expression for the solution for this ordinary differential equation. Fig. 2 shows a graphical representation for the state trajectory under the ESS's which has been computed numerically.

Figs. 3 and 4 represent the ESS as well as the value function as a function of state and time.

Fig. 3 clearly shows that the parental effort increases toward the end of the care period and decreases with the fitness level of the offspring. The latter effect is far more dramatic toward the end of the care period. In Fig. 4, we can clearly observe the boundary condition  $V(T, x) = x$  at the left-hand side.

## 6. State vs. energy dependent feedback strategies

In this section, we discuss whether parents may have an advantage, if they could condition their strategies not only on the level of offspring welfare, but also on the levels of energy reserves. Obviously, one can argue that energy expenditures and offspring well-fare are naturally linked, and that by observing its own energy levels and

the offspring well-fare the parent may well be able to deduce its partners energy expenditures and therefore energy levels. But in our deterministic setup we can even say more. In fact, we prove that it is only the knowledge of the offspring welfare, not the knowledge about its own energy levels, which is needed to implement the dynamic evolutionary strategy. We mention at this point, that the fact that our model is deterministic is crucial for the following consideration. In a stochastic model, where independent random effects influence the welfare of the offspring and the energy levels of the parents we expect this to change. Let us set up a dynamic differential parental care game, which allows for welfare and energy dependent strategies. In order to achieve this we have to extend the state equation of the differential game from Section 5 as follows :

$$\begin{aligned}\dot{X}(t) &= b(X(t), \varphi_1(t, X(t), E_1(t), E_2(t)) + \varphi_2(t, X(t), E_2(t), E_1(t))), \\ \dot{E}_i(t) &= -\frac{k}{2} \varphi_i(t, X(t), E_i(t), E_{-i}(t))^2\end{aligned}$$

for  $i = 1, 2$ . Here,  $E_i(t)$  represent the energy levels of parent  $i$  at time  $t$ . The payoff for parent  $i$  can now be represented by  $J^i = X(T) + E_i(T)$  which is exactly the same expression as in (17). The difference is that feedback strategies in this setup now not only depend on the offspring welfare but also on the energy-levels of both parents.

**Proposition 6.1.** *The ESS  $\varphi^*(t, x, e_1, e_2)$  of the differential parental care game presented above coincides with the ESS computed for the differential parental care game presented in Section 5, and as a consequence does not depend on the level of energy reserves  $e_1$  and  $e_2$ .*

**Proof.** In the formal setup of Section 3, we now have to set  $F \equiv 0$  and

$$f(s, x, y_1, y_2) = \left( (y_1 + y_2) \cdot g(x), -\frac{k}{2} y_1^2, -\frac{k}{2} y_2^2 \right)^T$$

as well as  $q^i(x, e_1, e_2) = x + e_i$ . Setting up the Hamilton–Jacobi–Bellman equation for the first parent and a symmetric feedback Nash-equilibrium  $\varphi^*(t, x, e_1, e_2)$  we obtain for the valuefunction  $V(t, x, e_1, e_2)$

$$\begin{aligned}-V_t(t, x, e_1, e_2) &= \max_u \left\{ V_x(t, x, e_1, e_2) \cdot (u + \varphi^*(t, x, e_2, e_1)) \cdot g(x) \right. \\ &\quad \left. + V_{e_1}(t, x, e_1, e_2) \cdot \left( -\frac{k}{2} u^2 \right) + V_{e_2}(t, x, e_1, e_2) \cdot \left( -\frac{k}{2} \varphi^*(t, x, e_2, e_1)^2 \right) \right\}\end{aligned}$$

with  $V(T, x, e_1, e_2) = x + e_1$ . Carrying out the maximization in the brackets gives

$$\varphi^*(t, x, e_1, e_2) = \frac{1}{k} \cdot \frac{V_x(t, x, e_1, e_2)}{V_{e_1}(t, x, e_1, e_2)} \cdot g(x). \quad (34)$$

By a symmetry argument we obtain for the second players strategy  $\varphi^*(t, x, e_2, e_1) = \frac{1}{k} \cdot \frac{V_x(t, x, e_2, e_1)}{V_{e_1}(t, x, e_2, e_1)} \cdot g(x)$  where  $V_{e_1}(t, x, e_2, e_1)$  denotes the partial derivative with respect to the third argument of the valuefunction of the first parent evaluated at  $(t, x, e_2, e_1)$ . Substituting these two expressions into the Hamilton–Jacobi–Bellman equation leads to

$$\begin{aligned}-V_t(t, x, e_1, e_2) &= \left( \frac{1}{k} \cdot \frac{V_x(t, x, e_1, e_2)^2}{V_{e_1}(t, x, e_1, e_2)} + \frac{1}{k} \cdot \frac{V_x(t, x, e_1, e_2) V_x(t, x, e_2, e_1)}{V_{e_1}(t, x, e_2, e_1)} \right. \\ &\quad \left. - \frac{1}{2k} \cdot \frac{V_x(t, x, e_1, e_2)^2}{V_{e_1}(t, x, e_1, e_2)} - \frac{1}{2k} V_{e_2}(t, x, e_1, e_2) \cdot \frac{V_x(t, x, e_2, e_1)^2}{V_{e_1}(t, x, e_2, e_1)} \right) \cdot g(x)^2.\end{aligned}$$

Uniqueness of a possible solution of the PDE follows again from [6, p. 77]. Let us try the following candidate for the solution of the PDE above. Define  $V(t, x, e_1, e_2) := \tilde{V}(t, x) + e_1$  where  $\tilde{V}(t, x)$  is a function which does not depend on  $e_1$  or  $e_2$ . Clearly, we have  $V_t = \tilde{V}_t$ ,  $V_x = \tilde{V}_x$ ,  $V_{e_1} = 1$ ,  $V_{e_2} = 0$ . Substituting this into the PDE derived above, we obtain a for the function  $\tilde{V}(t, x)$

$$-\tilde{V}_t(t, x) = \frac{3}{2k} \tilde{V}_x(t, x) \cdot g(x)^2.$$

The latter PDE is identical with (21), and represents the Hamilton–Jacobi–Bellman equation for the differential game, where strategies only depend on the offspring’s welfare. With the terminal condition  $\tilde{V}(T, x) = x$  we obtain  $V(T, x, e_1, e_2) = x + e_1$ . The statement of [Proposition 6.1.](#) now follows from Eq. (34), the fact that  $V_{e_1}(t, x, e_1, e_2) = 1$  and [Proposition 5.1.](#)  $\square$

## 7. A comparison with the static Houston–Davies parental care game

Let us now compare the ESS from the static Houston–Davies game as discussed in Section 2, but interpreted as a strategy in the differential game introduced in Section 5, and the ESS for the differential parental care game. We restrict our study to the case of [Example 5.1](#) but for other choices of the function  $g(\cdot)$ , qualitatively similar results can be obtained. We already demonstrated in Section 5 how the static Houston–Davies game from Section 2 can be embedded in our dynamic differential framework by considering the static strategies from the Houston–Davies game as dynamic feedback strategies which are constant in time and state. With the choice of  $g(x) = e^{-x}$  and quadratic costs as introduced in Section 5, we re-obtain exactly the version of the Houston–Davies game discussed in Section 2. We now consider the following three scenarios of possible parental care:

- *Scenario 1.* Both parents use the static Houston–Davies strategy.
- *Scenario 2.* One parent uses the static Houston–Davies strategy and one parent the dynamic ESS computed in Section 5.
- *Scenario 3.* Both parents use the dynamic ESS.

In order to see how these three scenarios qualitatively differ from each other let us first compare the state trajectories, which represent the offspring’s fitness as a function of time. [Fig. 5](#) displays the offspring’s fitness under each of the three scenarios for  $k = 1$ .

The dashed green line represents scenario 1, the dotted black line scenario 2 and the solid blue line scenario 3. Approximatively, all trajectories represent logarithmic growth. One can see, that the three curves do not intersect, except at  $t = 0$ . Furthermore, the offspring is obviously better off in scenario 1 than in scenario 3. More precisely, we have

**Proposition 7.1.** Denote with  $X_s(t)$ ,  $X_m(t)$  and  $X_d(t)$  the offspring’s fitness under scenario 1, 2 and 3, respectively. Then  $X_s(t) \geq X_m(t) \geq X_d(t)$  for all  $t \in [0, T]$ .

**Proof.** We only proof  $X_s(t) \geq X_d(t)$  for all  $t \in [0, T]$ . The inequalities  $X_s(t) \geq X_m(t)$  and  $X_m(t) \geq X_d(t)$  for all  $t \in [0, T]$  can be proved along the same line of arguments, but the formulas involved are much longer. Our proof consists of two parts. In the first part we show that in the initial phase  $X_s(\cdot)$  grows faster than  $X_d(\cdot)$ ,

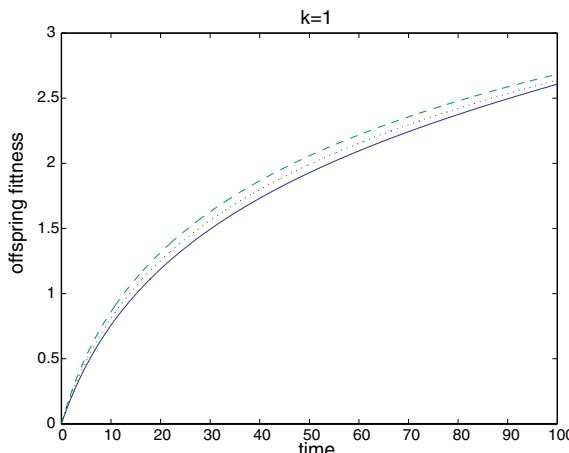


Fig. 5. Offspring fitness under different scenarios.

while in the second part we show, that once  $X_s(\cdot)$  is above  $X_d(\cdot)$  it remains above  $X_d(\cdot)$  forever. At time  $t = 0$  we have by definition  $X_d(t) = 0 = X_s(t)$ . The state dynamics under scenario 1 resp. scenario 3 are given as follows:

$$\begin{aligned}\dot{X}_s(t) &= \frac{\sqrt{1 + \frac{8T}{k}} - 1}{2T} \cdot e^{-X_s(t)}, \\ \dot{X}_d(t) &= \frac{2}{k} \frac{1}{\frac{1}{2}e^{X_d(t)} + \frac{1}{2}\sqrt{e^{2X_d(t)} + \frac{12}{k}(T-t)}} \cdot e^{-X_d(t)}.\end{aligned}$$

Let us write these two dynamics as  $\dot{X}_d(t) = f(t, X_d(t)) \cdot e^{-X_d(t)}$  and  $\dot{X}_s(t) = C(k) \cdot e^{-X_s(t)}$  where the function  $f(t, x)$  is given by  $f(t, x) = \frac{1}{k} \frac{4}{e^x + \sqrt{e^{2x} + \frac{12}{k}(T-t)}}$  and  $C(k) = \frac{\sqrt{1 + \frac{8T}{k}} - 1}{2T}$ . The differential equation for  $X_s(\cdot)$  can be solved analytical. The result is

$$X_s(t) = -\ln(2) + \ln \left( \frac{t \cdot \sqrt{1 + \frac{8T}{k}} - t + 2T}{T} \right). \quad (35)$$

The instantaneous growth rate at time  $t = 0$  for  $X_d(\cdot)$  is given by

$$f(0, 0) = \frac{1}{k} \frac{4}{1 + \sqrt{1 + \frac{12}{k}T}} =: D(k).$$

Now consider the function  $E(k) =: C(k) - D(k)$ . The derivative of  $E(k)$  with respect to  $k$  is given by the following expression:

$$E'(k) = \frac{-2}{\sqrt{1 + \frac{8T}{k}}k^2} + \frac{4}{\left(1 + \sqrt{1 + \frac{12T}{k}}\right)k^2} - \frac{24T}{k^3 \left(1 + \sqrt{1 + \frac{12T}{k}}\right)^2 \sqrt{1 + \frac{12T}{k}}}.$$

By a brute force computation one can show that this expression is always negative. The function  $E(k)$  is therefore strictly monotonic decreasing. Furthermore, it follows easily from its definition, that  $\lim_{k \rightarrow \infty} E(k) = \lim_{k \rightarrow \infty} C(k) - \lim_{k \rightarrow \infty} D(k) = 0 - 0 = 0$ . Therefore,  $E(k) \geq 0$  for all  $k \in [0, \infty)$  and hence  $C(k) \geq D(k)$ , for all  $k \in [0, \infty)$ . The latter inequality means that for all cost factors  $k$  the instantaneous growth rate of  $X_s(\cdot)$  at time  $t = 0$  is greater than the instantaneous growth rate of  $X_d(\cdot)$  at time  $t = 0$  and therefore that in the very beginning of the breeding process the offspring is better off under the static Houston–Davies strategy than under the dynamic evolutionary strategy. The second part of the proof becomes more technical and leads to very long and tedious computations, which we omit. We sketch the general idea however. Assume that there would exist a time  $t = t^*$  s.t.  $X_s(t^*) = X_d(t^*)$ . From Eq. (35), we then know that  $\dot{X}_d(t^*) = g_k(t^*) \cdot e^{-X_d(t^*)}$  with

$$g_k(t) = \frac{1}{k} \frac{4}{\left(1 + \frac{(\sqrt{1 + \frac{8T}{k}} - 1) \cdot t}{2T}\right) + \sqrt{\left(1 + \frac{(\sqrt{1 + \frac{8T}{k}} - 1) \cdot t}{2T}\right)^2 + \frac{12}{k} \cdot (T-t)}}.$$

We are done if we can show that  $g_k(t^*) \leq C(k)$  since then, even if the two trajectories would touch, the trajectory of  $X_d(\cdot)$  would remain below the trajectory of  $X_s(\cdot)$ . Eq. (35) would obviously be true if  $\max_{t \in [0, T]} g_k(t) \leq C(k)$ . In the first part of the proof we have already shown that  $g(0) = f(0, 0) = D(k) \leq C(k)$ . With a little bit more effort one can also show that  $g_k(T) \leq C(k)$  for all  $k \in [0, \infty)$ . Now, assuming that there exists an interior maximizer, one can use a first-order criterion to compute the potential maximizer  $t_{\max}$  and by brutal force computation show that  $g(t_{\max}) \leq C(k)$ . This proves the second part.  $\square$

The statement of the previous proposition may at first glance seem surprising and even confusing, but is not a contradiction to evolutionary theory, since the criterion is the payoffs for the parents, which includes not only the well being of the offspring, but also the individual costs. Nevertheless the result is very interesting, since it

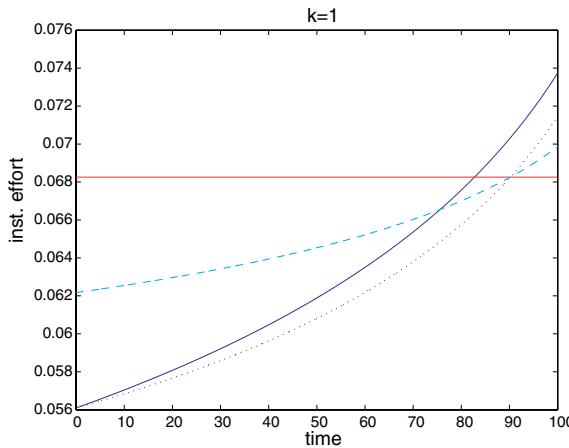


Fig. 6. Level of instantaneous effort under different scenarios.

Table 1

| Cost-factor $k$        | 1/4    | 1/2    | 1      | 2      |
|------------------------|--------|--------|--------|--------|
| Benefit $(d, d)$       | 3.2789 | 2.9412 | 2.6072 | 1.9564 |
| Benefit $(d, s)$       | 3.3117 | 2.9735 | 2.6387 | 1.9854 |
| Benefit $(s, s)$       | 3.3599 | 3.0207 | 2.6845 | 2.0267 |
| Dynamic costs $(d, d)$ | 0.2052 | 0.2024 | 0.1984 | 0.1854 |
| Dynamic costs $(d, s)$ | 0.1975 | 0.1949 | 0.1912 | 0.1792 |
| Static costs           | 0.4826 | 0.4756 | 0.4659 | 0.4341 |
| $J^2(d, d)$            | 3.0736 | 2.7388 | 2.4088 | 1.7709 |
| $J^2(d, s)$            | 2.8291 | 2.4979 | 2.1728 | 1.5513 |
| $J^1(d, s)$            | 3.1142 | 2.7786 | 2.4475 | 1.8061 |
| $J^1(s, s)$            | 2.8773 | 2.5450 | 2.2186 | 1.5925 |

says, that the young ones with sophisticated parents do worse than the young ones with unsophisticated parents. Fig. 6 shows the level of instantaneous efforts under different scenarios. The solid blue line displays the level of instantaneous effort provided by a parent which follows the dynamic ESS under scenario 3, which means that its partner also follows the dynamic ESS. The dotted black line also displays the level of instantaneous effort provided by a parent which follows the dynamic ESS, but this time under scenario 2, which means that its partner follows the static Houston–Davies rule. The solid red line displays the level of instantaneous effort provided by a parent which follows the static Houston–Davies rule. As this level is independent of the state of the offspring's fitness, it is the same in all three scenarios. Finally, the dashed cyan line displays the average of the solid red line and dotted black line and represents the effective level of instantaneous effort under scenario 2. Let also consider the payoffs for the different pairs of strategy profiles, which under an evolutionary dynamic determine which strategy thrives best in the population. Table 1 represents some key data for the different strategy profiles under the various pairings, including the final payoffs for different cost factors  $k$ .

Table 1 shows that in an essentially homogeneous population of individuals using the dynamic evolutionary strategy, individuals who use the static Houston–Davies strategy cannot invade, but that on the other side, an essentially homogeneous population of individuals using the static Houston–Davies strategy can be invaded by individuals using the more sophisticated dynamic evolutionary strategy. Noticing that  $J^1(d, s) = J^2(s, d)$  and  $J^1(s, s) = J^2(s, s)$  Table 1 above shows in fact that the dynamic evolutionary strategy is strictly dominant against the static Houston–Davies strategy.

## 8. Conclusions

While game theory has played an important part in evolutionary biology and theoretical ecology in the past, applications of differential games are clearly under-represented in the biological context. We introduced a first differential game model for the conflict over parental care. This model contains the classical Houston–Davies [4] model in a very natural way and can be seen as a continuous time dynamic version of the Houston–Davies model, which includes state dependent strategies. We solve this game for feedback Nash-equilibria by using Hamilton–Jacobi–Bellman theory as well as the method of characteristic curves. Though our model may seem to be rather simple, our approach is completely new to game theoretic modeling in biology. We also show that parents cannot obtain a significant advantage by conditioning their strategies on their energy levels in addition to the welfare of the offspring. We furthermore compare the newly obtained dynamic evolutionary strategy with the classical static Houston–Davies strategy and discuss issues like the well being of the offspring. We obtained the interesting result that the offspring with non-sophisticated parents, i.e. parents who use the static Houston–Davies rule, are better off than the offspring of sophisticated parents using the dynamic evolutionary strategy.

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## References

- [1] T.H. Clutton-Brock, The Evolution of Parental Care, Princeton University Press, Princeton, 1991.
- [2] E. Dockner, S. Jorgensen, N. Van Long, G. Sorger, Differential Games in Economic and Management Science, Cambridge University Press, 2000.
- [3] A. Grafen, R. Sibly, A model of mate desertion, *Anim. Behav.* 26 (1978) 645–652.
- [4] A.I. Houston, N.B. Davies, The evolution of cooperation and life history in the dunnock *Prunella modularis*, in: R.M. Sibly, R.H. Smith (Eds.), Behavioral Ecology, Blackwell Scientific Publications, 1985, pp. 471–487.
- [5] A. Houston, T. Szekely, J. McNamara, Conflict between parents over care, *Trends Ecol. Evol.* 20 (1) (2005).
- [6] J.D. Logan, An Introduction to Nonlinear Partial Differential Equations, Pure and Applied Mathematics, Wiley Interscience Series, 1994.
- [7] J. Maynard Smith, Parental investment: a prospective analysis, *Anim. Behav.* 25 (1977) 1–9.
- [8] J.M. McNamara et al., A dynamic game-theoretic model of parental care, *J. Theor. Biol.* 205 (2000) 605–623.
- [9] N. Yamamura, N. Tsuji, Parental care as a game, *J. Evol. Biol.* 6 (1993) 103–127.
- [10] D. Yeung, L. Petrosyan, Cooperative Stochastic Differential Games. Springer Series in Operations Research and Financial Engineering.

## Estimating the volume of a solid body

Professor Markus Reiss, Humboldt University of Berlin

<https://www.mathematik.hu-berlin.de/de/forschung/forschungsgebiete/stochastik/stoch-employees/mreiss>

Abstract: We are interested in estimating the volume of a solid body in  $\mathbb{R}^d$  based on observations of points uniformly distributed over the body and under minimal assumptions on the boundary like smoothness, convexity and  $r$ -convexity (the so-called rolling-ball condition). The main object of study is an estimator originally proposed in <http://arxiv.org/abs/1502.05510> for a slightly different problem. The performance of this estimator is yet to be understood for the class of  $r$ -convex bodies, but there is an increasing evidence that it works optimally. In this external project, our aim is to provide numerical and theoretical guarantees for the estimator.

This estimator can then be employed to estimate the volume of a patient's tumour. Typically we don't know the true shape of the tumour and have access to only some sort of measurements, often imprecise, like the detection of presence of the tumour in a certain region.

There is an evidence that the poisson point process is a suitable mathematical model for that. It turns out that one the main ingredients of proving the convergence rates of the estimator is to understand the asymptotic bound for the expected number of vertices of the  $r$ -convex hull and analyse how it depends on the curvature parameter  $r$ .

Thus the project can be split into 3 steps:

1. Adapt and evaluate numerically the performance of the estimator.
2. Derive an asymptotic bound for the expected number of vertices of the  $r$ -convex hull. Verify the bound numerically.
3. Employ statistical adaptation techniques to estimate the unknown curvature parameter  $r$ . Verify the results numerically.

A good starting point in investigating the  $r$ -convex hull is this paper  
<http://arxiv.org/pdf/1507.00065.pdf>

Project: Twinkling in sonar systems.

Dr P. Dobbins

Ultra Electronics Sonar Systems

Turbulence and other inhomogeneities in the water column cause fluctuations in propagating acoustic signals in the same way that turbulence in the interstellar medium causes stars to twinkle [1,2]. The amplitude fluctuations bring about signal fading and failure to detect targets well within the theoretical range of the system. Phase fluctuations, however, cause loss of directivity and angular resolution in receiving arrays, spreading of transmitted beams, variations in the apparent arrival direction of signals and fluctuations in their arrival time. Fluctuations also result in an occasional high peak in the signal amplitude, allowing sources or targets to be detected at ranges much greater than predicted by the conventional sonar equation [3]. The aim of this project will be to model the underwater medium as a random phase-changing screen [4] and predict the detection range that might be obtained using these occasional high peaks.

## References

- [1] Hewish, A., 1974. *Pulsars and High Density Physics*, Nobel Lecture.
- [2] Uscinski, B. J., 1977. *The Elements of Wave Propagation in Random Media*, McGraw-Hill.
- [3] Uscinski, B. J. and M. Spivack. 2005. High Intensity Ribbons in Multiply Scattering Media. *Waves in Random Media* 15(3) 339-352.
- [4] Buckley, R., 1975. Diffraction by a Random Phase-Changing Screen: a Numerical Experiment. *J. Atmos. Terr. Phys.* 37(11)1431-1457