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Kleptoparasitic Hawk-Dove Games

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Abstract
The Hawk-Dove game is a classical game-theoretical model of potentially aggressive animal conflicts. In this paper, we apply game theory to a population of foraging animals that may engage in stealing food from one another. We assume that the population is composed of two types of individuals, Hawks and Doves. Hawks try to escalate encounters into aggressive contests while Doves engage in non-aggressive displays between themselves or concede to aggressive Hawks. The fitness of each type depends upon various natural parameters, such as food density, the mean handling time of a food item, as well as the mean times of conflicts over the food. We find the Evolutionarily Stable States (ESSs) for all parameter combinations and show that there are two possible ESSs, pure Hawks, or a mixed population of Hawks and Doves. We demonstrate that for any set of parameter values there is exactly one ESS.

Keywords: Food stealing, kleptoparasitism, ESS, war of attrition, aggressive conflict

1 Introduction

The Hawk-Dove game was introduced in [37, 36] to model a potentially aggressive conflict over a shareable resource in a population where each individual can be exhibit one of the two strategies: Hawk or Dove. Upon encounter with another individual, both strategies start with displaying aggression. The Hawks then try to escalate into a real fight. The Dove, if faced with major escalation, retreats to safety. If not faced with such an escalation, i.e. in a Dove-Dove conflict, the Doves attempt to share the resource. For resources that cannot be shared, the Dove-Dove conflict was further extended into a war of attrition, a non-aggressive display of individuals where the winner is the one who displays longest [6, 28].

The applications of the Hawk-Dove game in biology are now widespread, see for example [15]. They include modelling of kleptoparasitism, a method of feeding in which an animal steals food that was found or prepared by another animal [38]. The kleptoparasitic behavior allows the stealing animal to obtain food without expending much energy to search for a source [7]. While kleptoparasitism is most commonly seen in seabirds with large food items and during periodic food shortages [7], it is also observed across many taxa [31] and in particular in mammals [32], fish [26], and insects [46, 17, 5, 19]. Kleptoparasitism is often crucial for the dynamics of various ecosystems [20, 34]. Kleptoparasitic interactions can be quite complex with animals exhibiting many different types of defending, fighting, and fleeing behavior, see [31] for a review.

Many game-theoretical models of kleptoparasitism now build on [13] and [10]. The original Hawk strategy morphed into a strategy that tries to steal and defends against a stealing attempt while the original Dove morphed into a strategy that does not attempt to steal and does not defend against stealing, see for example [11, 14, 12, 9, 21, 40, 45]. Also, many recent models contain a high degree of detail and realism, see for example [2, 3, 4, 24, 25, 22, 23] and also [39] or [30] for recent reviews.

In this paper, we try to return to the original interpretation of the strategies. We consider a population in which all individuals are trying to steal. Hawks also try to escalate the stealing attempt into an aggressive contest if met with resistance. Doves either cease the stealing attempt or give up the resource if met with a major escalation. If two Doves meet, they engage in a non-aggressive display modelled by the war of attrition. The model is motivated by blackbirds *Turdus merula*. Foraging blackbirds chase competitors away from the feeding area (aggressive behavior) and they also exhibit posturing displays between the two birds (war of attrition) [16]. A similar behavior was observed amongst oystercatchers *Haematopus ostralegus* feeding on mussels *Mytilus edulis* [42].

The paper is organized as follows. We set up the game in Section 2. We consider a Doves only population in Section 3.1, Hawks only population in Section 3.2, and a general mixed population in Section 3.3. We conclude our paper with a discussion in Section 4.

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2 Model

The basic structure of the model follows [12]. Individuals forage for food, and can be in one of the three behavioral stages: (1) a searcher looking for food items, (2) a handler preparing the food item for consumption, or (3) engaged in a pair-wise contest over the food item with another individual.

2.1 Types of individuals and behavioral stages

We consider a polymorphic population consisting of the two different types: aggressive Hawks and non-aggressive Doves. Each individual is initially searching for food items (at rate ν_f) or handlers (at rate ν_h).

The food density is f and so the searchers find food items at rate $\nu_f f$. Once they find the food item, the individual becomes a handler. The handling follows the shell model [11]; the food item is assumed to be something like an oyster that has to be removed from the shell. The time it takes to extract the food is unpredictable and variable from item to item. We assume that the handling time follows an exponential distribution with mean t_h. At the end of the handling period, the food item is instantaneously consumed, the handler receives a payoff of one unit and becomes a searcher again.

When a searcher finds a handler, the searcher tries to steal the food item. When a Hawks finds a Dove handler, the Hawk escalates and the Dove handler surrenders the food item and becomes a searcher while the Hawk becomes a handler. If the Hawk encounters a Hawk handler, the handler fights back and both the searcher and the handler engage in an aggressive conflict. The conflict times follow the exponential distribution with mean t_a. At the end of the fight, the winner becomes the handler and the loser becomes a searcher.

When a Dove searcher finds a Hawk handler, the Hawk defends the item and escalates the conflict almost immediately. The Dove retreats and resumes being a searcher while the Hawk resumes being the handler. If a Dove searcher finds a Dove handler, they engage in the war of attrition [35], a non-aggressive form of display. It is a classical result [6] that both Doves follow a strategy to display for the time drawn from the exponential distribution. Since the war of attrition lasts the minimum of the two times the individuals were prepared to wait, the average duration of this non-aggressive contest is half of their means and we will denote it by t_w. The individual that gives up first will become a searcher. The other individual will become a handler.

2.2 The dynamics of transitions between behavioral stages

We will assume that the total population has a density 1. By D, we will denote the density of the whole Dove population and by $H = 1 - D$, we will denote the density of the whole Hawk population. We denote by D_s, D_h, D_w the densities of Doves engaged in searching, handling and the war of attrition, respectively. Similarly, by H_s, H_h, H_a, we will denote the densities of Hawks engaged in searching, handling and aggressive contests.

The notation is summarized on Table 1. The transitions between different stages are shown in Figure 1 and the densities follow the following differential equations.

$$\frac{dD_s}{dt} = \left(t_h^{-1} + \nu_h H_s\right) D_h + \frac{D_w}{t_w} - (\nu_f f + \nu_h D_h) D_s \quad (1)$$

$$\frac{dD_h}{dt} = \nu_f f D_s + \frac{D_w}{t_w} - (t_h^{-1} + \nu_h H_s + \nu_h D_s) D_h \quad (2)$$

$$\frac{dD_w}{dt} = 2\nu_h D_h D_s - 2\frac{D_w}{t_w} \quad (3)$$

$$\frac{dH_s}{dt} = \frac{H_h}{t_h} + \frac{H_a}{t_a} - (\nu_f f + \nu_h D_h + \nu_h H_h) H_s \quad (4)$$

$$\frac{dH_h}{dt} = (\nu_f f + \nu_h D_h) H_s + \frac{H_a}{t_a} - (t_h^{-1} + \nu_h H_s) H_h \quad (5)$$

$$\frac{dH_a}{dt} = 2\nu_h H_h H_s - 2\frac{H_a}{t_a} \quad (6)$$

with

$$D = D_s + D_h + D_w \quad (7)$$

$$H = 1 - D = H_s + H_h + H_a. \quad (8)$$

To understand how the equations (1)–(6) were derived, we will comment on (1) in more details. A searching Dove either becomes a handler at the rate $\nu_f f$ or engages in the war of attrition at the rate $\nu_h D_h$. Since this is happening to every searching Dove, the density of searching Dove decreases at the rate $(\nu_f f + \nu_h D_h) D_s$. At the same time, a handling Dove becomes a searcher when attached by a searching Hawk, i.e., at the rate $\nu_h H_s$, or when finished handling at the rate t_h^{-1}. A Dove engaged in the war of attrition becomes a searcher when the war is finished, i.e. at the rate t_w^{-1}. Thus, the density of searching Doves increases at the rate $\left(t_h^{-1} + \nu_h H_s\right) D_h + t_w^{-1} D_w$. Putting it all together yields that the change of D_s, $\frac{dD_s}{dt}$, is as given in (1).

As in [11] and [33], we will assume that the population densities converge to equilibrium exponentially fast, and we thus concentrate on these equilibrium values only.

2.3 Payoffs

The fitness of the individuals will be evaluated as the benefits over the unit time [8, 44, 43].

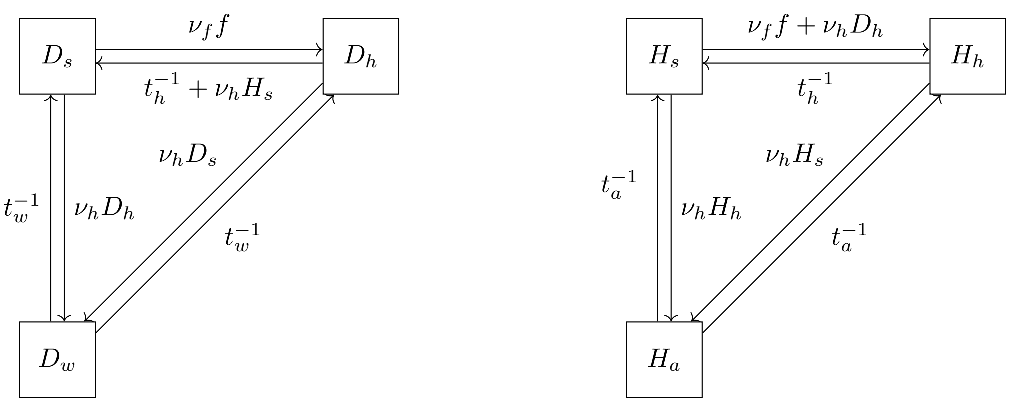

Figure 1: Phase diagram for Doves (left) and Hawks (right).

Table 1: Notation and model parameters

Symbol	Meaning
H	Total density of Hawks
H_s	Density of searching Hawks
H_h	Density of handling Hawks
H_a	Density of Hawks in aggressive contests
D	Total density of Doves
D_s	Density of searching Doves
D_h	Density of handling Doves
D_w	Density of Doves in wars of attrition
f	Density of the food items
ν_f	Rate at which searchers look for food
ν_h	Rate at which searchers look for handlers
t_h	Mean handling time
t_a	Mean duration of aggressive contests
t_w	Mean duration of wars of attrition

Assuming the population is in the equilibrium, an individual Dove spends a proportion D_h/D of the time as a handler, and during the handling time it acquires the benefits at the rate t_h^{-1}. The payoff to the Doves is thus given by

$$P_D = \frac{D_h}{t_h D}. \tag{9}$$

An individual Hawk spends a proportion H_h/H of the time as a handler acquiring benefits at the rate t_h^{-1}. The payoff to the Hawks is thus given by

$$P_H = \frac{H_h}{t_h H}. \tag{10}$$

2.4 Evolutionary stable states (ESSs)

We will investigate which mixtures of Hawks and Doves are evolutionarily stable [41, 36, 1, 29], i.e. satisfy the following conditions:

1. If both types are present in the mixture, then (a) they have an equal payoff and (b) a small increase of the proportion of one type lowers its payoff relative to the other type.
2. If only one type is present in the mixture and the other type somehow appears in very small numbers (with a density approaching 0), then the payoff of the rare type would be smaller than the payoff of the prevalent type.

2.5 Differences from [12]

Our model is an extension of [12]. We added a compartment D_w to explicitly include the possibility for non-aggressive contests, exhibited for example by foraging blackbirds during posturing displays [16]. With this addition, our model also more closely mimics the original game [37, 36]. We can still recover the model from [12] by setting t_w close to 0, i.e. by assuming the war of attrition between two Doves is resolved almost immediately.

At the same time, [12] assumed that Doves did not look for handlers and consequently could find the food faster than Hawks. While this assumption is logical, we did not consider this option as it did not seem happening in blackbirds [16] nor oystercatchers [42].

3 Analysis

The system (1)–(6) is too complex to be solved analytically. We will therefore start by considering the populations consisting either entirely of Doves or entirely of Hawks.

3.1 Dove only population

In the population without Hawks, the search for the equilibria of the system (1)–(6) reduces to solving the following algebraic equations

$$0 = \frac{D_h}{t_h} + \frac{D_w}{t_w} - (\nu_f f + \nu_h D_h) D_s \tag{11}$$

$$0 = \nu_f f D_s + \frac{D_w}{t_w} - (t_h^{-1} + \nu_h D_s) D_h \tag{12}$$

$$0 = 2\nu_h D_h D_s - 2\frac{D_w}{t_w} \tag{13}$$

$$1 = D_s + D_h + D_w. \tag{14}$$

By (13),

$$D_w = t_w \nu_h D_s D_h. \tag{15}$$

Subtracting (12) from (11) yields

$$D_s = (t_h \nu_f f)^{-1} D_h. \tag{16}$$

Substituting (15) and (16) into (14) yields

$$t_h \nu_f f = D_h(1 + t_h \nu_f f) + t_w \nu_h D_h^2. \tag{17}$$

Thus, setting $T = 1 + t_h \nu_f f$ yields

$$D_h = \begin{cases} \frac{T-1}{T}, & \text{if } t_w \nu_h = 0, \\ \frac{-T + \sqrt{T^2 + 4 t_w \nu_h (T-1)}}{2 t_w \nu_h}, & \text{otherwise.} \end{cases} \tag{18}$$

To summarize, the solution to the system (11)-(14) is given by (18), (16) and (15). Note that it follows from (18) that that D_h is decreasing form $\frac{t_h \nu_f f}{1 + t_h \nu_f f}$ to 0 as $t_w \nu_h$ increases from 0 to ∞.

Let us now check the conditions under which a population consisting of only Doves will be an ESS. Introducing a very small amount of Hawks into a population of Doves will not (significantly) change the payoff to Doves. To evaluate the payoff for Hawks, we need to evaluate H_h/H. Because there are only a few Hawks, there will be essentially no fights, i.e. we can assume $H_a = 0$ and thus $H_s + H_h = H$. Subtracting (5) from (4) and setting the time derivative to 0 yields

$$H_s = (t_h \nu_f f + t_h \nu_h D_h)^{-1} H_h \tag{19}$$

and thus

$$\frac{H_h}{H} = \frac{1}{1 + (t_h \nu_f f + t_h \nu_h D_h)^{-1}} \tag{20}$$

$$= \frac{t_h \nu_f f + t_h \nu_h D_h}{1 + t_h \nu_f f + t_h \nu_h D_h}. \tag{21}$$

Since $D_h > 0$, and the function $f(x) = \frac{x}{1+x}$ is increasing, we get

$$\frac{H_h}{H} > \frac{t_h \nu_f f}{1 + t_h \nu_f f} \geq \frac{D_h}{D}. \tag{22}$$

Consequently, a small number of Hawks will always do better in a population of Doves. Thus, Doves are never an ESS.

3.2 Hawk only population

In the population without Doves, the search for the equilibria of the system (1)–(6) reduces to solving

$$0 = \frac{H_h}{t_h} + \frac{H_a}{t_a} - (\nu_f f + \nu_h H_h) H_s \tag{23}$$

$$0 = \nu_f f H_s + \frac{H_a}{t_a} - (t_h^{-1} + \nu_h H_s) H_h \tag{24}$$

$$0 = 2\nu_h H_h H_s - 2\frac{H_a}{t_a} \tag{25}$$

$$1 = H_s + H_h + H_a. \tag{26}$$

By (25),

$$H_a = t_a \nu_h H_h H_s. \tag{27}$$

Subtracting (24) from (23) yields

$$H_s = (\nu_f f t_h)^{-1} H_h. \tag{28}$$

Substituting (28) and (27) into (26) yields

$$t_h \nu_f f = H_h + t_h \nu_f f H_h + t_a \nu_h H_h^2. \tag{29}$$

Thus, when we again set $T = 1 + t_h \nu_f f$,

$$H_h = \begin{cases} \frac{T-1}{T}, & \text{if } t_a \nu_h = 0, \\ \frac{-T + \sqrt{T^2 + 4 t_a \nu_h (T-1)}}{2 t_a \nu_h}, & \text{otherwise.} \end{cases} \tag{30}$$

To summarize, the solution to a system (23)-(26) is given by (30), (28) and (27).

Let us now check the conditions under which a population consisting of only Hawks will be an ESS. Introducing a small amount of Doves into the population will not change the payoffs to Hawks. Subtracting (2) from (1) and setting the time derivative to 0 yields

$$0 = \frac{D_h}{t_h} + \nu_h H_s D_h - \nu_f f D_s \tag{31}$$

and thus

$$D_s = D_h \frac{1 + t_h \nu_h H_s}{t_h \nu_f f}. \tag{32}$$

Since $D_s + D_h = D$ (as $D_w \approx 0$ since D is so small that $D_s D_h \approx 0$), we get

$$\frac{D_h}{D} = \frac{t_h \nu_f f}{1 + t_h \nu_f f + t_h \nu_h H_s} = \frac{t_h \nu_f f}{1 + t_h \nu_f f + \frac{\nu_h}{\nu_f f} H_h}. \tag{33}$$

Hawks do better than Doves if $H_h = H_h/H$ is bigger than D_h/D, i.e. if

$$H_h > \frac{t_h \nu_f f}{1 + t_h \nu_f f + \frac{\nu_h}{\nu_f f} H_h}, \tag{34}$$

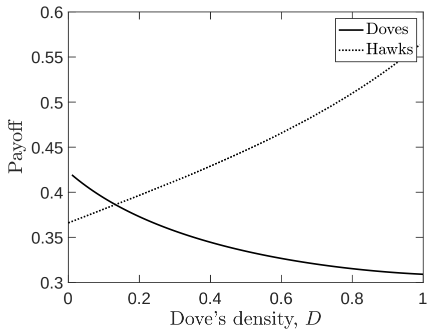

Figure 2: Payoff for Doves (solid) and Hawks (dotted) in an equilibrium as it depends on the density of Doves in the population, D. Values of other parameters are $\nu_h = 1, t_h = 1, t_w = 4, t_a = 2, \nu_f f = 1$. The value of D for which the payoffs intersect is ESS.

which is equivalent to

$$H_h^2 \frac{\nu_h}{\nu_f f} + H_h \left(1 + t_h \nu_f f\right) - t_h \nu_f f > 0 \tag{35}$$

which is, by (29), equivalent to

$$H_h^2 \nu_h \left(\frac{1}{\nu_f f} - t_a \right) > 0. \tag{36}$$

Consequently, Hawks do better than Doves if $t_a < \frac{1}{\nu_f f}$, i.e. when the time of the fight is smaller than the time to find a food item. If $t_a > \frac{1}{\nu_f f}$, the Doves can invade the Hawks.

3.3 General mixture

The analytical solution for the equilibrium of the full system (1)–(6) proved impossible as it yields to a quartic equation. Therefore, we set the left hand side of equations (1)–(6) to 0 and found solutions that also satisfied (7) and (8) numerically using Matlab. We did this for given values of parameters $\nu_f f$, ν_h, t_h, t_a and t_w and every Dove density $D \in \{0, 0.01, 0.02, \dots, 1\}$. We obtained four sets of solutions $(D_s, D_h, D_w, H_s, H_h, H_a)$. Two sets had imaginary components and one set had components outside $[0, 1]$. This allowed us to find a unique equilibrium of (1)–(6) with real values in $(0, 1)$ that also satisfied (7) and (8). We then calculated the payoff for Doves, P_D, and Hawks, P_H, as in (9) and (10), see Figure 2.

We observed that $P_H - P_D$ was increasing in D. From Section 3.1 we know that $P_H > P_D$ when $D = 1$. From Section 3.2 we know that $P_D < P_H$ when $D = 0$ and $t_a > \frac{1}{\nu_f f}$. Thus, there is only one ESS and the density of Doves in the ESS, D_{ESS} is either 0 when $t_a < \frac{1}{\nu_f f}$ or between 0 and 1 when $t_a > \frac{1}{\nu_f f}$.

The dependence of D_{ESS} parameter values is shown in Figure 3. D_{ESS} is increasing in $\nu_f f$ and t_a (unless $t_a < \frac{1}{\nu_f f}$ in which case $D_{\text{ESS}} = 0$). D_{ESS} is decreasing in t_w and also slightly decreasing in ν_h and t_h.

4 Conclusions and Discussion

In this paper we studied the population of foraging individuals that adopt one of the two strategies: aggressive Hawk or non-aggressive Dove. We studied how the density of Doves in an ESS depends on parameter values. This extended the original Hawk-Dove game [37, 36] to model kleptoparasitic interactions.

We saw that when $t_a < \frac{1}{\nu_f f}$, i.e. the mean duration of the aggressive contest is less than the expected time to find a food item, Hawk is an ESS. Otherwise, there is a unique mixed ESS. The density of Doves in the mixed ESS increases with increasing $\nu_f f$ (when food items are abundant and easy to find) and with t_a (when Hawks spend too much time in an aggressive contest). These results are in qualitative agreement with the original game [37, 36] as t_a could be seen as the cost of the aggressive contest and $\frac{1}{\nu_f f}$ represents the value of a food item. Similarly, the density of Doves in the mixed ESS decreases with t_w (when Doves spend more time in the non-aggressive war of attrition) and also slightly decrease with increasing t_h (when individuals stay longer as handlers) and ν_h (when handlers are easier to find).

Our model is a variation of a model from [12]. Unlike in our model which closely mimics the original game [37, 36], in [12] Doves did not attempt to steal. In our model, this could be achieved by choosing t_w close to 0, i.e. by assuming the war of attrition between two Doves is resolved almost immediately. At the same time, [12] assumed that Doves did not look for handlers and consequently could find the food faster than Hawks. Consequently, unlike in our model or in [37, 36], Doves alone could be ESS in [12] for some parameter values.

A stochastic variant of the Hawk-Dove game in a finite population was studied in [27], see also [18, 9]. While the stochastic models generally agree with the deterministic ones, the outcomes are much richer and the dependence on the parameter values is more complex than for the deterministic models.

Finally, we note that [11] considered other strategies such as including Retaliators who do not attempt to steal but aggressively defend the food items and Marauders who try to steal but do not defend. An addition of these two strategies made any Hawk-Dove mixture evolutionary unstable because it could be invaded either by Retaliators or by Marauders. It would be interesting to see what would happen in our model when these two strategies are introduced.

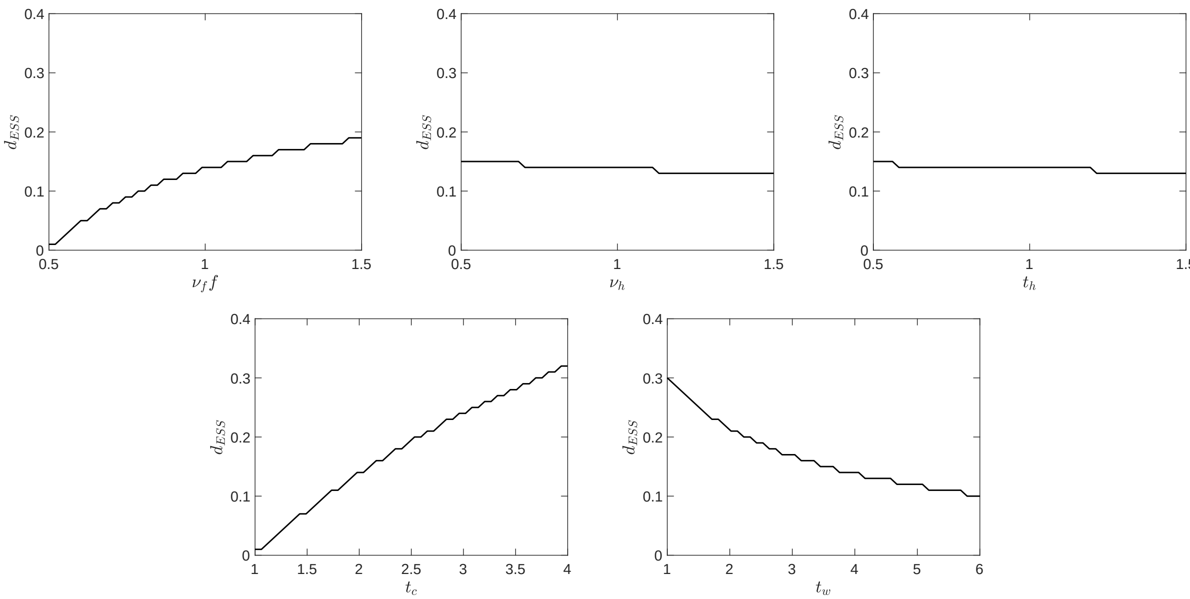

Figure 3: Density of Doves in ESS as it depends on different parameter values. When not changing, the values are $\nu_h = 1$, $t_h = 1$, $t_w = 4$, $t_a = 2$, $\nu_f f = 1$.

Author Contributions

I.H.E.: software, formal analysis, investigation, and writing - original draft
C.T.K.: software, formal analysis, investigation, and writing - original draft
K.L.O.: software, formal analysis, investigation, and writing - original draft
J.R.: writing - original draft, writing - review and editing, software, methodology, supervision, conceptualization
D.T.: writing - original draft, writing - review and editing, methodology, supervision, conceptualization, formal analysis

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