Journal of Theoretical Biology 483 (2019) 109993

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/jtb

Revisiting the “fallacy of averages” in ecology: Expected gain per unit time equals expected gain divided by expected time

Mark Broom[a], Ross Cressman[b], Vlastimil Křivan[c,d,*]

[a] Department of Mathematics, City, University of London, London, UK
[b] Department of Mathematics, Wilfrid Laurier University, Waterloo, Ontario, Canada
[c] Department of Mathematics, Faculty of Science, University of South Bohemia, Branišovská 1760, České Budějovice 370 05, Czech Republic
[d] Czech Academy of Sciences, Biology Centre, Institute of Entomology, Branišovská 31, České Budějovice 370 05, Czech Republic

ARTICLE INFO

Article history:
Received 18 January 2019
Revised 26 July 2019
Accepted 2 September 2019
Available online 3 September 2019

Keywords:
Diet choice model
Fallacy of averages
Functional response
Hamilton’s rule
Prisoner’s dilemma game

ABSTRACT

Fitness is often defined as the average payoff an animal obtains when it is engaged in several activities, each taking some time. We point out that the average can be calculated with respect to either the time distribution, or to the event distribution of these activities. We show that these two averages lead to the same fitness function. We illustrate this result through two examples from foraging theory, Holling II functional response and the diet choice model, and one game-theoretic example of Hamilton’s rule applied to the time-constrained Prisoner’s dilemma (PD). In particular, we show that in these models, fitness defined as expected gain per unit time equals fitness defined as expected gain divided by expected time. We also show how these fitnesses predict the optimal outcome for diet choice and the prevalence of cooperation in the repeated PD game.

1. Introduction

A key concept of evolutionary and behavioral ecology is fitness. Typically, individuals during their life are engaged in various activities with differential consequences on fitness that is then calculated as an average over these activities. Each of these activities may occur more than once and each occurrence takes some time. Fitness can then be calculated as the average payoff with respect to either the time distribution of the different activities or the number of different activity events. These two approaches can be controversial. One such controversy relates to optimal foraging theory (Pulliam, 1974; Charnov, 1976a; 1976b; Stephens and Krebs (1986)) where fitness (or a proxy of fitness) is defined as the average energy gained per average duration of foraging bout. Templeton and Lawlor (1981) argued that several papers on optimal foraging defined fitness as the average of energy intake per unit of time which is inconsistent with the formula given in these articles that expresses fitness as average energy gained per average foraging bout. They argued that such a “fallacy of the averages” is due to the fact that the expected value of the energy gained per unit time (denoted as $\mathrm{E}(\frac{G}{T})$ where G is the energy obtained in a time interval of length T) is not the expected gain divided by the expected time (denoted as $\frac{\mathrm{E}(G)}{\mathrm{E}(T)}$).

To see clearly the problem in question, Stephens and Krebs (1986) provide the following example, with a forager in a three patch environment. An individual can either go to patch 1 and stay there for 8 minutes and obtain 5 units of food (choice 1), or it can go first to patch 2, an empty patch, and stay there for 3 minutes and then go to patch 3 for 5 minutes and obtain there 6 units of food (choice 2). For the first choice $\mathrm{E}(\frac{G}{T}) = \frac{\mathrm{E}(G)}{\mathrm{E}(T)} = \frac{5}{8}$. For the second choice $\mathrm{E}(\frac{G}{T}) = \frac{3}{5} < \frac{\mathrm{E}(G)}{\mathrm{E}(T)} = \frac{3}{4}$. With these expected values, the optimal choice for the forager depends on how fitness is defined for choice 2. That is, if fitness is taken as $\mathrm{E}(\frac{G}{T})$ (respectively $\frac{\mathrm{E}(G)}{\mathrm{E}(T)}$), then choice 1 (respectively, choice 2) is optimal.

Turelli et al. (1982) argued that the Templeton and Lawlor (1981) fallacy of averages had not been committed because these authors incorrectly interpreted results of the articles they criticized. Finally, Gilliam et al. (1982) showed that no fallacy of averages was committed by Charnov (1976b) because expected value of the quotient equals the quotient of the expected values when probability spaces are chosen correctly in his foraging model. Indeed, in the above example, the expected values for choice 2 are calculated with respect to the probability space that has two events, A (empty patch 2) and B (patch 3), each with probability $\frac{1}{2}$. That is, $\mathrm{E}(\frac{G}{T}) = \frac{1}{2} \times 0 + \frac{1}{2} \times \frac{6}{5} = \frac{3}{5}$ and $\frac{\mathrm{E}(G)}{\mathrm{E}(T)} = \frac{\frac{1}{2}\times 0+\frac{1}{2}\times 6}{\frac{1}{2}\times 3+\frac{1}{2}\times 5} = \frac{3}{4}$. The

---

[*] Corresponding author.

E-mail addresses: mark.broom.1@city.ac.uk (M. Broom), rcressman@wlu.ca (R. Cressman), vlastimil.krivan@gmail.com (V. Křivan).

https://doi.org/10.1016/j.jtbi.2019.109993

above probability distribution for calculating $\mathrm{E}(\frac{G}{T})$ is incorrect. Instead, the probability of event A (respectively, event B) here should be the probability the forager is in the empty patch (respectively, patch 3) when a time between 0 and 8 minutes is chosen at random. These probabilities are then $\frac{3}{8}$ and $\frac{5}{8}$, respectively. This results in $\mathrm{E}(\frac{G}{T}) = \frac{3}{8} \times 0 + \frac{5}{8} \times \frac{6}{5} = \frac{3}{4}$, which is the same as $\frac{\mathrm{E}(G)}{\mathrm{E}(T)}$ for choice 2 with respect to the original probability space. That is, the expected gain per unit of time, $\mathrm{E}(\frac{G}{T})$, equals expected gain divided by expected time, $\frac{\mathrm{E}(G)}{\mathrm{E}(T)}$, when these expected values are calculated with respect to the correct probability distributions.

We should note that the fallacy of averages described above is related to Jensen's inequality (Jensen, 1906), where in general $\mathrm{E}(f(X)) \le (\ge) f(\mathrm{E}(X))$ if f is a concave (convex) function. For example the fact that $\log(X)$ is a concave function implies that the geometric mean is never greater than the arithmetic mean for positive-valued X. In the case we consider there is a similar inequality caused by a failure to correct for the appropriate usage of probability spaces when evaluating fitness in two distinct ways.

Let us consider an individual with two activities that we call activity 1 and activity 2 (this is easily extended to the case with an arbitrary number of activities, see the Appendix). Now consider a time interval $T = T_1 + T_2$ where T_i is the total time the individual spends in activity i. The probability distribution of these activity times is then $(t_1, t_2) = (T_1/T, T_2/T)$. We define our fitness (proxy) Π as the average (with respect to the distribution of activity times $t = (t_1, t_2)$) energy gain per time. That is,

$$\Pi = \mathrm{E_t}\left(\frac{G}{T}\right) = \frac{\pi_1}{\tau_1}\frac{T_1}{T} + \frac{\pi_2}{\tau_2}\frac{T_2}{T} = \frac{\pi_1}{\tau_1}t_1 + \frac{\pi_2}{\tau_2}t_2, \tag{1}$$

where $\mathrm{E_t}$ is the expectation operator with respect to the distribution of activity times, π_i is the energy gain of a single event of activity i and τ_i is the time this event takes.

Now we consider the distribution of activity events. Let m_i be the number of times event i takes place in a time interval T. Then the distribution of activity events is $(e_1, e_2) = (m_1/M, m_2/M)$ (where $M = m_1 + m_2$). Since $T_i = m_i\tau_i$ and $T = m_1\tau_1 + m_2\tau_2$, the relationship between the distribution of activity times and the distribution of activity events is given by

$$t_i = \frac{m_i\tau_i}{m_1\tau_1 + m_2\tau_2} = \frac{e_i\tau_i}{e_1\tau_1 + e_2\tau_2}.$$

Thus,

$$\Pi = \mathrm{E_t}\left(\frac{G}{T}\right) = \frac{\pi_1}{\tau_1}t_1 + \frac{\pi_2}{\tau_2}t_2 = \frac{e_1\pi_1 + e_2\pi_2}{e_1\tau_1 + e_2\tau_2} = \frac{\mathrm{E_e}(G)}{\mathrm{E_e}(T)}, \tag{2}$$

where $\mathrm{E_e}$ is the expectation operator with respect to the distribution of activity events (Fig. 1).

In this article, we begin by briefly illustrating the equivalence of $\mathrm{E_t}(\frac{G}{T})$ and $\frac{\mathrm{E_e}(G)}{\mathrm{E_e}(T)}$ through applying the method to the development of the well-known Holling II functional response (Holling, 1959) and to the diet choice model (Charnov, 1976a). We then provide a more comprehensive treatment of a third application that generalizes Hamilton's rule (Hamilton, 1963; Broom and Rychtář, 2013) on the evolution of cooperation to the repeated Prisoner's dilemma game when the number of rounds played depends on strategy choice. As pointed out there and in the Discussion, the equivalent ways to calculate rate of gain have renewed importance for more recent behavioral models that include the effects of activity times. In all three examples, we show how to calculate either the time or the event distribution, which is the crucial component in determining an individual's gain rate.

2. Holling type II functional response

For the Holling II functional response, we consider two activities of a predator: searching for a prey, and handling a prey. Because searching for a prey is always followed by handling a prey, the number of searching events (m_1) and handling events (m_2) must be the same $(m_1 = m_2)$ and so half the events are handling and the other half are searching, i.e., $e_1 = e_2 = 1/2$ is the distribution of events. Moreover, from the searching activity event the predator does not gain any energy, $\pi_1 = 0$, while handling a prey item provides energy gain $\pi_2 = E$. Thus

$$\Pi = \frac{\mathrm{E_e}(G)}{\mathrm{E_e}(T)} = \frac{\frac{1}{2}0 + \frac{1}{2}E}{\frac{1}{2}\tau_s + \frac{1}{2}h} = \frac{E}{\tau_s + h}, \tag{3}$$

where we assume that on average it takes time $\tau_1 = \tau_s$ to find a prey and time $\tau_2 = h$ to handle the prey. If x denotes the number of prey and λ is the predator search rate, a searching predator encounters on average λx prey per unit time and $\tau_1 = \tau_s = 1/(\lambda x)$. Then

$$\Pi = \frac{E\lambda x}{1 + \lambda h x}$$

is the rate of energy intake based on the Holling type II functional response that measures the expected number of prey consumed by the predator per unit time (Holling, 1959). We note that the distribution of activity times is now

$$t_1 = \frac{m_1\tau_1}{m_1\tau_1 + m_2\tau_2} = \frac{m_1/(\lambda x)}{m_1/(\lambda x) + m_1 h} = \frac{1}{1 + \lambda h x}$$

and

$$t_2 = \frac{m_2\tau_2}{m_1\tau_1 + m_2\tau_2} = \frac{m_1 h}{m_1/(\lambda x) + m_1 h} = \frac{\lambda h x}{1 + \lambda h x}.$$

In this example, it was trivial to obtain the distribution of events, due to the sequential nature of searching for and handling of prey items. In general, the distribution of events and/or times can be more complicated or more difficult to calculate, as we will demonstrate in the following two examples.

3. The diet choice model of optimal foraging theory

The diet choice model (Charnov, 1976a) for two types of prey considers a predator searching for prey in an environment with prey types a and b. Let us assume that there are x_i $(i = a, b)$ prey type i in the environment. Also assume the predator has the same search rate λ for both types and cannot encounter more than one prey at a time. Then, during a total search time T_1, the predator encounters $T_1\lambda(x_a + x_b)$ prey, of which $T_1\lambda x_a$ (respectively, $T_1\lambda x_b$) are type a (respectively, type b).

Upon encountering a prey type $i = a, b$, the predator either starts to "handle" the prey with probability u_i, or starts a new search for another prey. Immediately after handling a prey item the predator starts searching for a new prey. Thus, there are three activities of a predator: searching for a prey (activity 1), handling prey type a (activity 2), and handling prey type b (activity 3). In time interval T, a predator either searches for a prey (which takes time T_1), or handles prey type a (T_2), or prey type b (T_3), i.e., $T = T_1 + T_2 + T_3$. If it takes h_i time units to handle a single prey of type i (i.e. $\tau_2 = h_a$, $\tau_3 = h_b$), then $T_2 = \lambda u_a x_a h_a T_1$ and $T_3 = \lambda u_b x_b h_b T_1$. Thus, $T_1 = T/(1 + \lambda u_a h_a x_a + \lambda u_b h_b x_b)$, from which the distribution of activity times $(\frac{T_1}{T}, \frac{T_2}{T}, \frac{T_3}{T})$ follows easily.

Let E_a and E_b be energy gains from handling one prey a or b item, respectively (i.e. $\pi_2 = E_a$, $\pi_3 = E_b$). Also, $\pi_1 = 0$ since the predator does not get any energy during searching. Thus, the predator's fitness defined as average energy gain per unit time is given by

$$\Pi = \mathrm{E_t}\left(\frac{G}{T}\right) = \frac{\pi_1}{\tau_1}\frac{T_1}{T} + \frac{\pi_2}{\tau_2}\frac{T_2}{T} + \frac{\pi_3}{\tau_3}\frac{T_3}{T} = \frac{\lambda u_a x_a E_a + \lambda u_b x_b E_b}{1 + \lambda u_a x_a h_a + \lambda u_b x_b h_b} \tag{4}$$

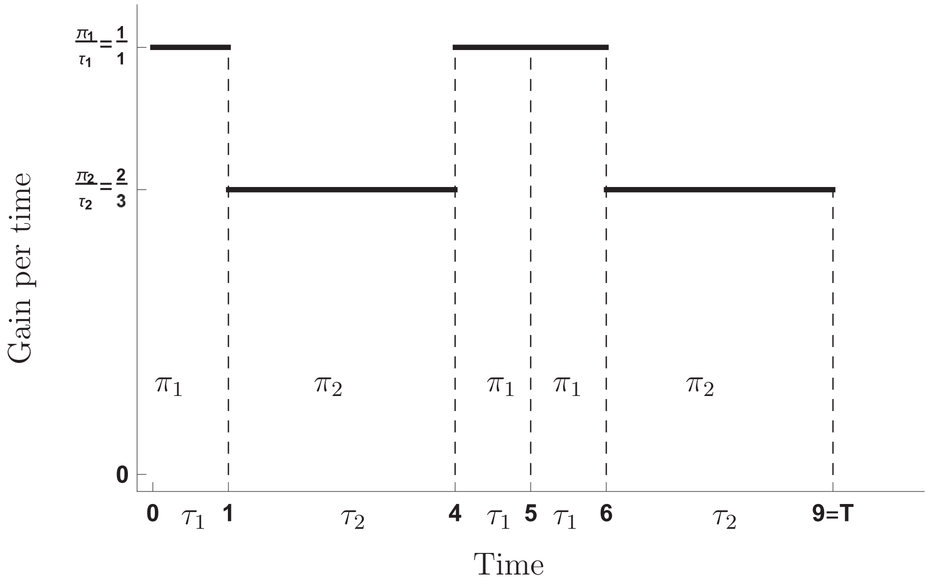

Fig. 1. Illustration of formulas (1) and (2). In this example there are two activities with energy gain per event $\pi_1 = 1$ and $\pi_2 = 2$. Also, in time interval $T = 9$, there are three activity 1 events and two activity 2 events with each event taking time $\tau_1 = 1$ and $\tau_2 = 3$, respectively. Thus the distribution of activity times is $(t_1, t_2) = (1/3, 2/3)$ and so the average energy gain per unit time is $1 \times 1/3 + 2/3 \times 2/3 = 7/9$ as in (1). The distribution of activity events is $(e_1, e_2) = (3/5, 2/5)$. The area below the graph of the function is the total energy gain $\mathrm{E_e}(G) = 3\pi_1 + 2\pi_2 = 7$ obtained in the total time T, so $\Pi = 7/9$ as in (2).

which extends Eq. (1) to three activities. Eq. (4) is the well-known formula for fitness used in the diet choice model of optimal foraging (Charnov, 1976a; Stephens and Krebs, 1986).

As emphasized in this article, the fitness is also given through the distribution of activity events. Specifically, in the time interval T, there are $m_1 = T_1\lambda(x_a + x_b)$ searches, $m_2 = T_1\lambda u_a x_a$ prey a handled and $m_3 = T_1\lambda u_b x_b$ prey b handled events. Since the search time for one prey is $\tau_s = 1/(\lambda(x_a + x_b))$ (cf. Holling type II functional response),

$$\Pi = \frac{\mathrm{E_e}(G)}{\mathrm{E_e}(T)} = \frac{m_1 0 + m_2 E_a + m_3 E_b}{m_1 \frac{1}{\lambda(x_a + x_b)} + m_2 h_a + m_3 h_b} = \frac{T_1\lambda u_a x_a E_a + T_1\lambda u_b x_b E_b}{T_1 + T_1\lambda u_a x_a h_a + T_1\lambda u_b x_b h_b}. \qquad (5)$$

The equivalence of (4) and (5) was pointed out by Gilliam et al. (1982) using different notation.

To maximize Π, the predator will handle all prey items it encounters that are most profitable (i.e., $u_a = 1$ if we assume that $\frac{E_a}{h_a} > \frac{E_b}{h_b}$) and will handle all (respectively, none) of prey type b it encounters if the density x_a of prey type a is below (respectively, above) the positive threshold level of $\frac{E_b}{\lambda(E_a h_b - E_b h_a)}$ (Charnov, 1976a; Stephens and Krebs, 1986). As shown in Cressman et al. (2014), this optimal outcome of foraging theory can be interpreted as the game-theoretic solution where the predator faces a decision tree and chooses the Nash equilibrium solution.

The following example applies similar game-theoretic reasoning in a more traditional setting.

4. Fitness in the repeated Prisoner's dilemma game: Hamilton's rule

One fallacy of averages mentioned by Templeton and Lawlor (1981) is Hamilton's rule that altruistic behavior is favored in models of kin selection when $\frac{\text{Loss of individual fitness}}{\text{Gain in relative's fitness}}$ is less than the degree of relatedness. This is related to cooperation and defection in the repeated Prisoner's dilemma (PD) game.

The single shot PD assumes that when two individuals interact, they have two strategies, either to cooperate, or to defect. If an individual cooperates, it pays cost c and gives benefit $b > c > 0$ to its partner.[1] If it defects, it does not pay the cost. The single shot PD game has the payoff matrix

$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \left[\begin{array}{cc} b - c & -c \\ b & 0 \end{array}\right] \end{array} \qquad (6)$$

where the matrix entries give the payoff to the row player when interacting with the column player. Thus, any player prefers to play against a cooperator rather than against a defector. So, if each player in an interacting pair is free to decide whether to continue the interaction or not, it can be assumed that a pair of cooperators want to stay together as long as possible while all other pairs will disband after one round. This leads us to consider the repeated Prisoner's dilemma where the same players play the single shot PD game for several rounds.

In our repeated PD game there are two types of players, Cooperators and Defectors. When two cooperators meet, their interaction lasts for $\tau > 1$ rounds and that their cumulative payoff is $\pi_{CC} \equiv (b - c)\tau$ for each of them. On the other hand, when a Defector meets either a Cooperator or another Defector, the interaction lasts one round. The payoff matrix per interaction is then

$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \left[\begin{array}{cc} \pi_{CC} & \pi_{CD} \\ \pi_{DC} & \pi_{DD} \end{array}\right] \end{array} = \begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \left[\begin{array}{cc} (b - c)\tau & -c \\ b & 0 \end{array}\right] \end{array} \qquad (7)$$

where the payoffs are given for the row player. We also assume that, between rounds, individuals from disbanded pairs, (i.e., those players whose interactions has ended) form new pairs at random.

Fitnesses[2] for the two strategies are taken as average payoffs per round with each round lasting one unit of time. Let us

---

[1] With these parameters, Hamilton's rule is that altruistic behavior is favored when $\frac{c}{b} < r$, where r measures the degree of relatedness.

[2] In this section we change terminology to the more traditional one used in evolutionary game theory. That is, instead of energy gain we use payoff and instead of average gain rate we use fitness.

consider the fitness of a cooperator[3]. In each round, this cooperator has two activities; namely, it is either paired with a cooperator or with a defector. Let T_{CC} (respectively T_{CD}) be the total time (i.e., the number of rounds) that the cooperator is paired with a cooperator (respectively, defector) in $T = T_{CC} + T_{CD}$ rounds, i.e., in the time interval T. That is, the distribution of the cooperator's activity times is $(t_{CC}, t_{CD}) = (T_{CC}/T, T_{CD}/T)$ and so the fitness of a cooperator, Π_C is

$$\Pi_C = \mathrm{E_t}\left(\frac{G}{T}\right) = \frac{\pi_{CC}}{\tau}\frac{T_{CC}}{T} + \frac{\pi_{CD}}{1}\frac{T_{CD}}{T} = (b-c)\frac{T_{CC}}{T} - c\frac{T_{CD}}{T}. \tag{8}$$

We can also consider the distribution of activity events (e_{CC}, e_{CD}) for the cooperator. Let m_{CC} (respectively, m_{CD}) be the number of interactions the cooperator has with a cooperator (respectively, defector) in a time interval T. Then the cooperator's distribution of activity events is $(e_{CC}, e_{CD}) = (m_{CC}/M, m_{CD}/M)$ (where $M = m_{CC} + m_{CD}$). Since $t_{CC} = \frac{m_{CC}\tau}{m_{CC}\tau + m_{CD}} = \frac{e_{CC}\tau}{e_{CC}\tau + e_{CD}}$ and $t_{CD} = \frac{m_{CD}}{m_{CC}\tau + m_{CD}} = \frac{e_{CD}}{e_{CC}\tau + e_{CD}}$,

$$\Pi_C = \mathrm{E_t}\left(\frac{G}{T}\right) = \frac{\pi_{CC}}{\tau}t_{CC} + \frac{\pi_{CD}}{1}t_{CD} = \frac{e_{CC}\pi_{CC} + e_{CD}\pi_{CD}}{e_{CC}\tau + e_{CD}} = \frac{\mathrm{E_e}(G)}{\mathrm{E_e}(T)}. \tag{9}$$

That is, the cooperator's fitness is given either as the expected payoff per round (with respect to the cooperator's distribution of activity times) or as the expected payoff divided by expected time (with respect to the cooperator's distribution of activity events).

To calculate fitness from (9), we need to know one of the activity distributions of the cooperator as a function of the number of cooperators n_C and the number of defectors n_D in the population. To this end, we assume that the distribution of activity times is given through the equilibrium of the discrete-time pair formation process that describes changes in the number of pairs as in Zhang et al. (2016). We note that in this example the CC interaction time τ affects both the payoffs from such an interaction and the overall distribution of the interacting pairs.

Let $n_{CC}(t)$ be the number of cooperator pairs (i.e., CC pairs), $n_{CD}(t)$ be the number of CD pairs and $n_{DD}(t)$ be the number of DD pairs at round t. With random pairing of disbanded singles between rounds, the distributional dynamics is then

$$\begin{aligned}
n_{CC}(t+1) &= \left(1 - \frac{1}{\tau}\right)n_{CC}(t) + \frac{\left(\frac{2n_{CC}(t)}{\tau} + n_{CD}(t)\right)^2}{4\left(\frac{n_{CC}(t)}{\tau} + n_{CD}(t) + n_{DD}(t)\right)},\\
n_{CD}(t+1) &= \frac{2\left(\frac{2n_{CC}(t)}{\tau} + n_{CD}(t)\right)(n_{CD}(t) + 2n_{DD}(t))}{4\left(\frac{n_{CC}(t)}{\tau} + n_{CD}(t) + n_{DD}(t)\right)},\\
n_{DD}(t+1) &= \frac{(n_{CD}(t) + 2n_{DD}(t))^2}{4\left(\frac{n_{CC}(t)}{\tau} + n_{CD}(t) + n_{DD}(t)\right)}.
\end{aligned} \tag{10}$$

For example, the number of cooperating pairs in the next round equals the number of continuing pairs $(1 - \frac{1}{\tau})n_{CC}$ plus the number of newly formed pairs (Zhang et al., 2016; Křivan and Cressman, 2017). These authors show that for $\tau \neq 1$,[4] (10) has a unique equilibrium

$$\begin{aligned}
n_{CC} &= \frac{n_C(2\tau - 1) + n_D - \sqrt{4n_C n_D\tau + (n_C - n_D)^2}}{4(\tau - 1)},\\
n_{CD} &= \frac{\sqrt{4n_C n_D\tau + (n_C - n_D)^2} - n_C - n_D}{2(\tau - 1)},\\
n_{DD} &= \frac{n_C + n_D(2\tau - 1) - \sqrt{4n_C n_D\tau + (n_C - n_D)^2}}{4(\tau - 1)}.
\end{aligned}$$

The distribution of activity times for a cooperator are then $t_{CC} = \frac{2n_{CC}}{2n_{CC} + n_{CD}}$ and $t_{CD} = \frac{n_{CD}}{2n_{CC} + n_{CD}}$. The fitness functions evaluated at this distribution are

$$\begin{aligned}
\Pi_C &= \left(\frac{n_C(2\tau - 1) + n_D - \sqrt{(n_C - n_D)^2 + 4n_C n_D\tau}}{2n_C(\tau - 1)}\right)b - c,\\
\Pi_D &= \left(\frac{\sqrt{(n_C - n_D)^2 + 4n_C n_D\tau} - n_C - n_D}{2n_D(\tau - 1)}\right)b,
\end{aligned} \tag{11}$$

when $\tau \neq 1$. We note that, for $\tau = 1$, the fitness functions are those of the classic one-shot PD game, $\Pi_C = \frac{n_C}{N}b - c$ and $\Pi_D = \frac{n_C}{N}b$, where it is always better to defect than cooperate. These classic payoffs can be found directly by assuming Eq. (10) is in equilibrium using $\tau = 1$, or taking the limit of Eq. (11) as τ tends to 1.

When the population size $N \equiv n_C + n_D$ is fixed, the above fitnesses define a two-strategy time-constrained (population) game. Defect is always a (pure-strategy) Nash equilibrium (NE) of this game (since $0 = \Pi_D > \Pi_C = -c$ when $n_D = N$). On the other hand, Cooperate is never a NE since $b = \Pi_D > \Pi_C = b - c$ when $n_C = N$. However, for $\tau \geq \frac{(b+c)^2}{(b-c)^2}$, there exist other mixed strategy NE which are found by solving $\Pi_C = \Pi_D$. These are given by (Křivan and Cressman 2017; see also Zhang et al., 2016)

$$\begin{aligned}
(n_C, n_D) &= \left(\frac{1}{2}N\left(1 - \frac{\sqrt{\tau(b-c)^2 - (b+c)^2}}{\sqrt{\tau - 1}(b-c)}\right),\right.\\
&\qquad \left.\frac{1}{2}N\left(1 + \frac{\sqrt{\tau(b-c)^2 - (b+c)^2}}{\sqrt{\tau - 1}(b-c)}\right)\right),\\
(n_C, n_D) &= \left(\frac{1}{2}N\left(1 + \frac{\sqrt{\tau(b-c)^2 - (b+c)^2}}{\sqrt{\tau - 1}(b-c)}\right),\right.\\
&\qquad \left.\frac{1}{2}N\left(1 - \frac{\sqrt{\tau(b-c)^2 - (b+c)^2}}{\sqrt{\tau - 1}(b-c)}\right)\right).
\end{aligned} \tag{12}$$

They also showed that the second mixed NE in (12) with the larger proportion of cooperators is stable when $\tau > \frac{(b+c)^2}{(b-c)^2}$ in the sense that $\Pi_C > \Pi_D$ (respectively, $\Pi_C < \Pi_D$) when the proportion of cooperators is slightly less (respectively, slightly more) than at this NE. That is, Hamilton's rule generalizes to the time-constrained PD game to state that selection favors the coexistence of cooperators and defectors when the interaction between cooperators lasts a sufficient number of rounds, which is independent of genetic relatedness.

5. Discussion

In this article, we consider the problem of calculating fitnesses in ecology in an appropriate and consistent manner. We show that fitness calculated as expected gain per unit time equals fitness calculated as expected gain divided by expected time provided probability spaces are chosen correctly. We apply this approach to three fundamental models of population and evolutionary ecology. In the first model, the two activities of an individual predator are searching for a prey and then handling it when encountered, leading in a natural way to fitness given through the Holling type II functional response when all prey are of the same type. In the second model, the diet choice of optimal foraging with two prey types, an individual predator has three different activities; namely, searching for a prey, handling prey type one or handling prey type two. In the third model, the repeated Prisoner's dilemma, where

---

[3] The fitness of a Defector is calculated analogously.

[4] For $\tau = 1$, the distribution of pairs is given by $(n_{CC}, n_{CD}, n_{DD}) = \left(\frac{n_C^2}{2(n_C+n_D)}, \frac{n_C n_D}{n_C+n_D}, \frac{n_D^2}{2(n_C+n_D)}\right)$ where pair proportions are given by the Hardy–Weinberg formula (e.g., the proportion of CC pairs among all pairs is $\frac{n_C^2}{(n_C+n_D)^2}$ and the number of all pairs is $(n_C + n_D)/2$).

the number of rounds is strategy dependent, the game's solution based on Nash equilibria leads to a version of Hamilton's rule predicting when selection favors cooperative behavior.

In all three models, we explicitly show that the fitnesses whether they are calculated as average gain per time, or average gain over average time lead to the same outcome when averaging is taken with respect to the distribution of activity times or the distribution of activity events, respectively. However, as illustrated by the third model, the challenging problem when calculating fitnesses can be to describe the distribution of activity times or activity events. This becomes more problematic in multi-strategy time-constrained games, including those that involve searching times in the pair formation process, where analytic expressions for these distributions are often unavailable. Nevertheless, in several recent articles on these general models, it has been shown, either by generalizing the distributional dynamics approach of Example 3 (e.g., Křivan and Cressman, 2017; Cressman and Křivan, 2019) or by using Markov methods (e.g., Garay et al., 2017; 2018), that the distributions still exist and are unique as functions of strategy numbers. The resultant fitness functions then define a population game that can be solved numerically if their analytic formulas are intractable.

A series of papers that also involve time delays and similar types of calculations are the game-theoretic kleptoparasitism models starting with Broom and Ruxton (1998) (see also Broom et al. (2004, 2008)). Here individuals could find their own food or steal from others, and were faced with strategic decisions about whether to challenge for food items, or to concede items when challenged. Individuals chose strategies to minimise the expected time for them to consume an item; thinking of an activity event as the sequence of actions until an item is consumed, the payoff is then effectively that from (2) where by definition $\mathrm{E_e}(G)=1$ and $\mathrm{E_e}(T)$ is the expected consumption time. Payoffs were also calculated in an equivalent way too, through finding the handling ratio, the proportion of individuals handling a food item at any time. Since food could only be consumed when in the handling state, the payoff per unit time was simply the handling ratio multiplied by the handling rate, which is a special case of Eq. (1).

The methodology that we have described can generalise to more complex scenarios where a number of different events are possible, each with their own distinct durations and rewards, and often with restrictions on the sequence in which they can occur. A natural area to consider is life history theory (Roff, 1992; Stearns, 1992), where trade-offs between times in distinct stages of life, and relative investment in different aspects such as reproduction and growth, are both common and often complicated. Here the scenario is generally not so simple as to maximise the expected reward functions (1) or (2), but there is potential to adapt the ideas we have developed here to consider more general situations. As a rule the more complex the model, the greater the scope for erroneous thinking when evaluating fitness. As we have considered in this paper, even apparently straightforward situations can be perilous.

In summary, foraging situations can be modeled either by considering the expected gain per unit time, or the expected gain per foraging event. Some modeling situations lend themselves to the first approach, some to the second. In this paper we have shown that when properly considered, these two methods are entirely equivalent and consequently researchers can be appropriately flexible in their approach.

Acknowledgments

This project has received funding from the European Union Horizon 2020 research and innovation program under the Marie Sklodowska-Curie grant agreement No 690817. VK acknowledges support provided by the Institute of Entomology (RVO:60077344) and RC by an NSERC of Canada Individual Discovery grant 7822. We also thank the two referees and the Handling Editor for their encouraging comments on the original submission.

Appendix A. Equivalence of payoffs with respect to time and event distributions

Let us consider $i=1,\dots,I$ events, each taking time τ_i. The payoff from each event is π_i, and the number of times each event takes place is m_i.

Consider the following three forms (A and B are similar in appearance, C somewhat different) of fitness payoff/fitness functions.

$$\text{Payoff } A=\frac{\sum_{i=1}^{I} m_i\pi_i}{\sum_{i=1}^{I} m_i\tau_i},$$

that is, the total reward from all events divided by the total time. Dividing all terms by the total number of events

$$M=\sum_{i=1}^{I} m_i$$

we obtain

$$\text{Payoff } B=\frac{\sum_{i=1}^{I} \frac{m_i}{M}\pi_i}{\sum_{i=1}^{I} \frac{m_i}{M}\tau_i},$$

where m_i/M is the proportion of events of type i.

We can rearrange payoff A in another way

$$\text{Payoff } C=\frac{\sum_{i=1}^{I} m_i\pi_i}{\sum_{i=1}^{I} m_i\tau_i}=\sum_{i=1}^{I}\frac{m_i\tau_i}{\sum_{j=1}^{I} m_j\tau_j}\,\frac{\pi_i}{\tau_i}.$$

Here the term $\frac{m_i\tau_i}{\sum_{j=1}^{I} m_j\tau_j}$ in the sum is the proportion of time spent in event i.

We note that Payoff B is written as the reward per interaction weighted by the proportion of interactions, and Payoff C is the reward per time weighted by the proportion of time. There are two plausible mistakes that can be made when calculationg the payoff. The example from Stephens and Krebs (1986) gives two different payoffs. $E(G)/E(T)$ is just Payoff B above, and so also equivalent to Payoff C. Their other payoff $E(G/T)$ gives a different value as we have discussed. This makes the mistake of using reward per time weighted by proportion of interactions. The reverse bias, which uses reward per interaction weighted by proportion of time, is a well known concept in renewal theory, "length-biased sampling" (Qin, 2017). Here individuals that live/stay longer (or are larger) are more likely to be observed and lead to estimation bias (although the bias can be corrected for as long as the researcher is aware of it, Lehnen, 2005).

References

Broom, M., Luther, R.M., Ruxton, G.D., 2004. Resistance is useless? - Extensions to the game theory of kleptoparasitism. Bull. Math. Biol. 66, 1645–1658.

Broom, M., Luther, R.M., Ruxton, G.D., Rychtář, J., 2008. A game-theoretic model of kleptoparasitic behavior in polymorphic populations. J. Theor. Biol. 255, 81–91.

Broom, M., Ruxton, G.D., 1998. Evolutionarily stable stealing: game theory applied TO kleptoparasitism. Behav. Ecol. 9, 397–403.

Broom, M., Rychtář, J., 2013. Game-Theoretical Models in Biology. CRC Press, Taylor & Francis Group, Boca Raton, FL.

Charnov, E.L., 1976. Optimal foraging: attack strategy of a mantid. Am. Nat. 110, 141–151.

Charnov, E.L., 1976. Optimal foraging: the marginal value theorem. Theor. Popul. Biol. 9, 129–136.

Cressman, R., Křivan, V., 2019. Bimatrix games that include interaction times alter the evolutionary outcome: the owner–intruder game. J. Theoret. Biol. 460, 262–273.

Cressman, R., Křivan, V., Brown, J.S., Gáray, J., 2014. Game-theoretical methods for functional response and optimal foraging behavior. PLoS ONE 9, e88773.

Garay, J., Cressman, R., Móri, T.F., Varga, T., 2018. The ESS and replicator equation in matrix games under time constraints. J. Math. Biol. 76, 1951–1973.

Garay, J., Csiszár, V., Móri, T.F., 2017. Evolutionary stability for matrix games under time constraints. J. Theor. Biol. 415, 1–12.
Gilliam, J.F., Green, R.F., Pearson, N.E., 1982. The fallacy of the traffic policeman: a response to templeton and Lawlor. Am. Nat. 119, 875–878.
Hamilton, W.D., 1963. The evolution of altruistic behavior. Am. Nat. 97.
Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. Can. Entomol. 91, 385–398.
Jensen, J.L.W.V., 1906. Sur les fonctions convexes et les inégalités entre les valeurs moyennes. Acta Math. 30, 175–193.
Křivan, V., Cressman, R., 2017. Interaction times change evolutionary outcomes: two player matrix games. J. Theoret. Biol. 416, 199–207.
Lehnen, S., 2005. Turnover rates of fall-migrating pectoral sandpipers in the lower mississippi alluvial valley. J. Wildl. Manage. 69, 671–680.
Pulliam, H.R., 1974. On the theory of optimal diets. Am. Nat. 108, 57–74.
Qin, J., 2017. Biased Sampling, Over-Identified Parameter Problems and Beyond. Springer Verlag, Singapore.
Roff, D.A., 1992. The Evolution of Life Histories: Theory and Analysis. Chapman and Hall, New York, NY, USA.
Stearns, S.T., 1992. The Evolution of Life Histories. Oxford University Press, Oxford.
Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press.
Templeton, A.R., Lawlor, L.R., 1981. The fallacy of the averages in ecological optimization theory. Am. Nat. 117, 390–393.
Turelli, M., Gillespie, J.H., Schoener, T.W., 1982. The fallacy of the fallacy of the averages in ecological optimization theory. Am. Nat. 119, 879–884.
Zhang, B.-Y., Fan, S.-J., Li, C., Zheng, X.-D., Bao, J.-Z., Cressman, R., Tao, Y., 2016. Opting out against defection leads to stable coexistence with cooperation. Sci. Rep. 6 (35902), 35902.