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

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## 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.

*Keywords:* Diet choice model, fallacy of averages, functional response, Hamilton’s rule, Prisoner’s dilemma game.

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## 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  
 20 respect to either the time distribution of the different activities or the number  
 of different activity events. These two approaches can be controversial. One  
 22 such controversy relates to optimal foraging theory (Pulliam, 1974; Charnov,  
 1976a,b; Stephens and Krebs, 1986) where fitness (or a proxy of fitness) is  
 24 defined as the average energy gained per average duration of foraging bout.  
 Templeton and Lawlor (1981) argued that several papers on optimal forag-  
 26 ing 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  
 28 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  
 30 energy gained per unit time (denoted as  $E(\frac{G}{T})$  where  $G$  is the energy obtained  
 in a time interval of length  $T$ ) is not the expected gain divided by the  
 32 expected time (denoted as  $\frac{E(G)}{E(T)}$ ).

To see clearly the problem in question, Stephens and Krebs (1986) provide  
 34 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  
 36 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  
 38 there 6 units of food (choice 2). For the first choice  $E(\frac{G}{T}) = \frac{E(G)}{E(T)} = \frac{5}{8}$ . For the  
 second choice  $E(\frac{G}{T}) = \frac{3}{5} < \frac{E(G)}{E(T)} = \frac{3}{4}$ . With these expected values, the optimal  
 40 choice for the forager depends on how fitness is defined for choice 2. That  
 is, if fitness is taken as  $E(\frac{G}{T})$  (respectively  $\frac{E(G)}{E(T)}$ ), then choice 1 (respectively,  
 42 choice 2) is optimal.

Turelli et al. (1982) argued that the Templeton and Lawlor (1981) fallacy  
 44 of averages had not been committed because these authors incorrectly inter-  
 preted results of the articles they criticized. Finally, Gilliam et al. (1982)  
 46 showed that no fallacy of averages was committed by Charnov (1976b) be-  
 cause expected value of the quotient equals the quotient of the expected  
 48 values when probability spaces are chosen correctly in his foraging model.  
 Indeed, in the above example, the expected values for choice 2 are calculated  
 50 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,  $E(\frac{G}{T}) = \frac{1}{2} \times 0 + \frac{1}{2} \times \frac{6}{5} = \frac{3}{5}$   
 52 and  $\frac{E(G)}{E(T)} = \frac{\frac{1}{2} \times 0 + \frac{1}{2} \times 6}{\frac{1}{2} \times 3 + \frac{1}{2} \times 5} = \frac{3}{4}$ . The above probability distribution for calcu-  
 lating  $E(\frac{G}{T})$  is incorrect. Instead, the probability of event A (respectively,  
 54 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  
56 random. These probabilities are then  $\frac{3}{8}$  and  $\frac{5}{8}$  respectively. This results in  
 $E(\frac{G}{T}) = \frac{3}{8} \times 0 + \frac{5}{8} \times \frac{6}{5} = \frac{3}{4}$ , which is the same as  $\frac{E(G)}{E(T)}$  for choice 2 with  
58 respect to the original probability space. That is, the expected gain per unit  
of time,  $E(\frac{G}{T})$ , equals expected gain divided by expected time,  $\frac{E(G)}{E(T)}$ , when  
60 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  
62 Jensen's inequality (Jensen, 1906), where in general  $E(f(X)) \leq (\geq) f(E(X))$   
64 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  
66 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  
68 of probability spaces when evaluating fitness in two distinct ways, which we  
elaborate on below.

Let us consider an individual with two activities that we call activity 1  
70 and activity 2 (this is easily extended to the case with an arbitrary number  
72 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  
74 distribution of these activity times is then  $(t_1, t_2) = (T_1/T, T_2/T)$ . We define  
our fitness (proxy)  $\Pi$  as the average (with respect to the distribution of  
76 activity times  $t = (t_1, t_2)$ ) energy gain per time. That is,

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

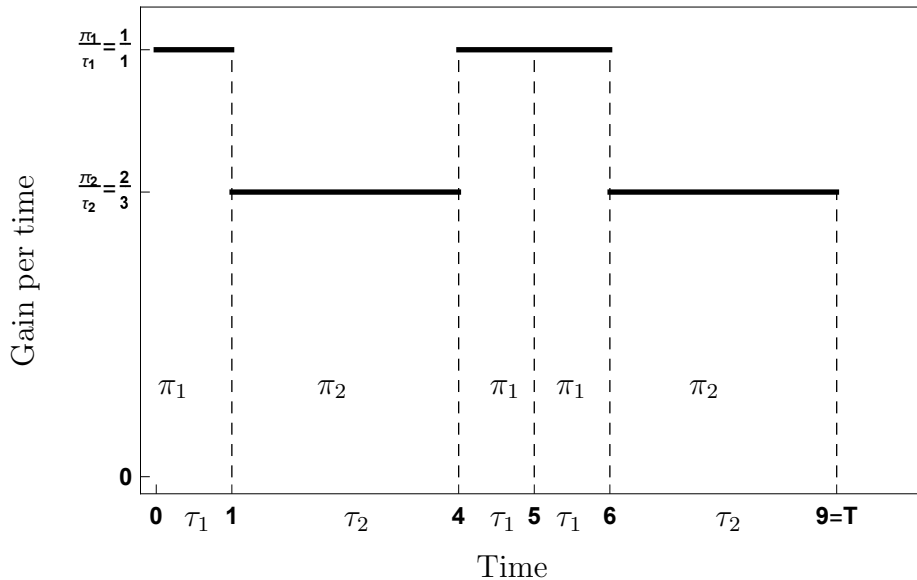
78 where  $E_t$  is the expectation operator with respect to the distribution of ac-  
tivity times,  $\pi_i$  is the energy gain of a single event of activity  $i$  and  $\tau_i$  is the  
80 time this event takes.

Now we consider the distribution of activity events. Let  $m_i$  be the number  
82 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  
84  $T_i = m_i \tau_i$  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

$$86 \quad t_i = \frac{m_i \tau_i}{m_1 \tau_1 + m_2 \tau_2} = \frac{e_i \tau_i}{e_1 \tau_1 + e_2 \tau_2}.$$

Thus,

$$88 \quad \Pi = E_t \left( \frac{G}{T} \right) = \frac{\pi_1}{\tau_1} t_1 + \frac{\pi_2}{\tau_2} t_2 = \frac{e_1 \pi_1 + e_2 \pi_2}{e_1 \tau_1 + e_2 \tau_2} = \frac{E_e(G)}{E_e(T)} \quad (2)$$



**Figure 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  $E_e(G) = 3\pi_1 + 2\pi_2 = 7$  obtained in the total time  $T$ , so  $\Pi = 7/9$  as in (2).

where  $E_e$  is the expectation operator with respect to the distribution of activity events.

In this article, we begin by briefly illustrating the equivalence of  $E_t\left(\frac{G}{T}\right)$  and  $\frac{E_e(G)}{E_e(T)}$  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.

### 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

106 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  
 108 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  
 110 the predator does not gain any energy,  $\pi_1 = 0$ , while handling a prey item  
 provides energy gain  $\pi_2 = E$ . Thus

$$112 \quad \Pi = \frac{E_e(G)}{E_e(T)} = \frac{\frac{1}{2}0 + \frac{1}{2}E}{\frac{1}{2}\tau_s + \frac{1}{2}h} = \frac{E}{\tau_s + h} \quad (3)$$

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

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

118 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  
 120 unit time (Holling, 1959). We note that the distribution of activity times is  
 now

$$122 \quad t_1 = \frac{m_1\tau_1}{m_1\tau_1 + m_2\tau_2} = \frac{m_1/(\lambda x)}{m_1/(\lambda x) + m_1h} = \frac{1}{1 + \lambda h x}$$

and

$$124 \quad t_2 = \frac{m_2\tau_2}{m_1\tau_1 + m_2\tau_2} = \frac{m_1h}{m_1/(\lambda x) + m_1h} = \frac{\lambda h x}{1 + \lambda h x}.$$

In this example, it was trivial to obtain the distribution of events, due to  
 126 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  
 128 difficult to calculate, as we will demonstrate in the following two examples.

### The Diet Choice model of Optimal Foraging Theory

130 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  
 132 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  $\lambda$  for both types and cannot  
 134 encounter more than one prey at a time. Then, during a total search time

136  $T_1$ , 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  $b$ ).

138 Upon encountering a prey type  $i = a, b$ , the predator either starts to  
 138 “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  
 140 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  
 142 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.,  
 144  $T = T_1 + T_2 + T_3$ . 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,  
 146  $T_1 = T / (1 + \lambda u_a h_a x_a + \lambda u_b h_b x_b)$ , from which the distribution of activity times  
 ( $\frac{T_1}{T}$ ,  $\frac{T_2}{T}$ ,  $\frac{T_3}{T}$ ) follows easily.

148 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  
 150 not get any energy during searching. Thus, the predator’s fitness defined as  
 average energy gain per unit time is given by

$$152 \quad \Pi = E_t \left( \frac{G}{T} \right) = \frac{\pi_1 T_1}{\tau_1 T} + \frac{\pi_2 T_2}{\tau_2 T} + \frac{\pi_3 T_3}{\tau_3 T} = \frac{\lambda u_a x_a E_a + \lambda u_b x_b E_b}{1 + \lambda u_a x_a h_a + \lambda u_b x_b h_b} \quad (4)$$

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

156 As emphasized in this article, the fitness is also given through the distri-  
 bution of activity events. Specifically, in the time interval  $T$ , there are  $m_1 =$   
 158  $T_1\lambda(x_a + x_b)$  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  $\tau_s = 1/(\lambda(x_a + x_b))$   
 160 (cf. Holling type II functional response),

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

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

164 To maximize  $\Pi$ , 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  
 166 (respectively, none) of prey type  $b$  it encounters if the density  $x_a$  of prey type

168  $a$  is below (respectively, above) the positive threshold level of  $\frac{E_b}{\lambda(E_a h_b - E_b h_a)}$   
 170 (Charnov, 1976a; Stephens and Krebs, 1986). As shown in Cressman et al.  
 172 (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.

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

### 174 **Fitness in the repeated Prisoner's dilemma game: Hamilton's rule**

176 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  
 178 to cooperation and defection in the repeated Prisoner's dilemma (PD) game.

180 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.<sup>1</sup> If it defects, it does  
 182 not pay the cost. The single shot PD game has the payoff matrix

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

184 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  
 186 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  
 188 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  
 190 Prisoner's dilemma where the same players play the single shot PD game for  
 several rounds.

192 In our repeated PD game there are two types of players, Cooperators  
 and Defectors. When two cooperators meet, their interaction lasts for  $\tau > 1$   
 194 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

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



196 Defector, the interaction lasts one round. The payoff matrix per interaction  
 is then

$$198 \quad \begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \left[ \begin{array}{cc} \pi_{CC} & \pi_{CD} \\ \pi_{DC} & \pi_{DD} \end{array} \right] = \begin{array}{c} C \\ D \end{array} \left[ \begin{array}{cc} (b-c)\tau & -c \\ b & 0 \end{array} \right] \end{array} \quad (7)$$

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

202 Fitnesses<sup>2</sup> for the two strategies are taken as average payoffs per round  
 with each round lasting one unit of time. Let us consider the fitness of a  
 204 cooperator<sup>3</sup>. In each round, this cooperator has two activities; namely, it is  
 either paired with a cooperator or with a defector. Let  $T_{CC}$  (respectively  $T_{CD}$ )  
 206 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  
 208 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,  $\Pi_C$   
 210 is

$$\Pi_C = \text{E}_t \left( \frac{G}{T} \right) = \frac{\pi_{CC}}{\tau} \frac{T_{CC}}{T} + \frac{\pi_{CD}}{1} \frac{T_{CD}}{T} = (b-c) \frac{T_{CC}}{T} - c \frac{T_{CD}}{T}. \quad (8)$$

212 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  
 214 cooperator has with a cooperator (respectively, defector) in a time interval  
 $T$ . Then the cooperator's distribution of activity events is  $(e_{CC}, e_{CD}) =$   
 216  $(m_{CC}/M, m_{CD}/M)$  (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  $t_{CD} = \frac{m_{CD}}{m_{CC}\tau + m_{CD}} = \frac{e_{CD}}{e_{CC}\tau + e_{CD}},$

$$218 \quad \Pi_C = \text{E}_t \left( \frac{G}{T} \right) = \frac{\pi_{CC}}{\tau} t_{CC} + \frac{\pi_{CD}}{1} t_{CD} = \frac{e_{CC}\pi_{CC} + e_{CD}\pi_{CD}}{e_{CC}\tau + e_{CD}} = \frac{\text{E}_e(G)}{\text{E}_e(T)}. \quad (9)$$

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

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<sup>2</sup>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.

<sup>3</sup>The fitness of a Defector is calculated analogously.

224 To calculate fitness from (9), we need to know one of the activity dis-  
 225 tributions of the cooperator as a function of the number of cooperators  $n_C$   
 226 and the number of defectors  $n_D$  in the population. To this end, we assume  
 227 that the distribution of activity times is given through the equilibrium of the  
 228 discrete-time pair formation process that describes changes in the number  
 229 of pairs as in Zhang et al. (2016). We note that in this example the CC  
 230 interaction time  $\tau$  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  
 232 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  
 234 dynamics is then

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

236 For example, the number of cooperating pairs in the next round equals the  
 237 number of continuing pairs  $(1 - \frac{1}{\tau})n_{CC}$  plus the number of newly formed pairs  
 238 (Zhang et al., 2016; Krivan and Cressman, 2017). These authors show that

for  $\tau \neq 1$ ,<sup>4</sup> (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 equation (10) is in equilibrium using  $\tau = 1$ , or taking the limit of equation (11) as  $\tau$  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

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<sup>4</sup>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  $(n_C + n_D)/2$ ).

by (Křivan and Cressman 2017; see also Zhang et al., 2016)

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

256 They also showed that the second mixed NE in (12) with the larger pro-  
 258 portion 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  
 260 (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  
 262 coexistence of cooperators and defectors when the interaction between coop-  
 erators lasts a sufficient number of rounds, which is independent of genetic  
 264 relatedness.

## Discussion

266 In this article, we consider the problem of calculating fitnesses in ecology  
 in an appropriate and consistent manner. We show that fitness calculated as  
 268 expected gain per unit time equals fitness calculated as expected gain divided  
 by expected time provided probability spaces are chosen correctly. We apply  
 270 this approach to three fundamental models of population and evolutionary  
 ecology. In the first model, the two activities of an individual predator are  
 272 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  
 274 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  
 276 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,  
 278 where 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  
 280 selection favors cooperative behavior.

In all three models, we explicitly show that the fitnesses whether they are  
 282 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  
 284 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  $E_e(G) = 1$  and  $E_e(T)$  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 equation (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  
324 the expected gain per unit time, or the expected gain per foraging event.  
Some modeling situations lend themselves to the first approach, some to  
326 the second. In this paper we have shown that when properly considered,  
these two methods are entirely equivalent and consequently researchers can  
328 be appropriately flexible in their approach.

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

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

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

342 
$$\text{Payoff A} = \frac{\sum_{i=1}^I m_i \pi_i}{\sum_{i=1}^I m_i \tau_i},$$

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

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

346 we obtain

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

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

We can rearrange payoff A in another way

350 
$$\text{Payoff C} = \frac{\sum_{i=1}^I m_i \pi_i}{\sum_{i=1}^I m_i \tau_i} = \sum_{i=1}^I \frac{m_i \tau_i}{\sum_{j=1}^I m_j \tau_j} \frac{\pi_i}{\tau_i}.$$

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  
352  $i$ .

We note that Payoff B is written as the reward per interaction weighted by  
354 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  
356 made when calculating the payoff. The example from Stephens and Krebs  
(1986) gives two different payoffs.  $E(G)/E(T)$  is just Payoff B above, and  
358 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  
360 weighted by proportion of interactions. The reverse bias, which uses reward  
per interaction weighted by proportion of time, is a well known concept  
362 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  
364 to estimation bias (although the bias can be corrected for as long as the  
researcher is aware of it, Lehnen, 2005).

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