The ratio versus difference optimization and its implications for optimality theory

Sonali Shinde,[1] **Ankur Patwardhan,**[1] **and Milind Watve**[2,3] (iD)

[1]*Annasaheb Kulkarni Department of Biodiversity, Abasaheb Garware College, Pune 411004, India*

[2]*Independent Researcher, Pune 411052, India*

[3]*E-mail: milind.watve@gmail.com*

Among the classical models of optimization, some models maximize the ratio of returns to investment and others maximize the difference between returns and investment. However, an understanding of under what conditions the ratio or the difference approaches are appropriate is still fragmentary. Under specific contexts, it has been stated that when the investable amount, but not the opportunity for investment, is perceived to be limiting, a ratio optimum is appropriate, whereas a difference optimum is appropriate when the opportunity for investment, but not the investable amount, is perceived to be limiting. The question is important because the strategies indicated by ratio optimum can be substantially different than the ones suggested by difference optimum. We make a general case here to examine and expand this principle and apply it to many evolutionary ecological problems including parental investment, offspring quality-quantity trade-off, nectar production, pollinator behavior viral burst size, and intracellular protein handling. We show that the ratio-difference distinction in optimization models resolves many long-standing debates and conundrums in evolution and behavior.

KEY WORDS: Difference optimum, offspring quality-quantity trade-off, optimality theory, parental investment, pollination, ratio optimum.

Optimality theory is an important element of behavioral ecology that assumes that a strategy that optimizes benefits in the face of costs gets selected. Optimization models can improve our understanding about adaptation and innate behavioral tendencies (Parker and Maynard Smith 1990). A number of examples of behavioral optimization are abound in the literature in behavioral ecology (Stephens & Krebs 1987; Ramírez-Bautista *et al.*, 2000; Thakar *et al.*, 2003; Ha 2010; Doniol-Valcroze *et al.*, 2011). Far fewer studies attempt convergence of proximate and ultimate causes in optimization and show that the proximate mechanisms achieve the adaptive purpose (Budaev *et al.*, 2019; Baig *et al.*, 2019). Nevertheless, at a conceptual level, optimization theory continues to be useful to address certain kinds of evolutionary, behavioral, and economics questions (Rahnev & Denison 2018). Despite limitations, constraints, and contextuality, optimization is a useful fundamental concept in behavioral ecology as well as in economics.

However, there are certain fundamental questions in optimality theory that remain incompletely understood. In foraging theory, it is recognized that there is more than one way of optimization and that the choice of the model is context dependent. For example, while optimizing the energy required for moving between foraging bouts the lapwing should move until the marginal benefit from the next step becomes equal to the marginal cost of the step (Parker and Maynard Smith1990). This maximizes the difference between the benefit function and cost. In another situation, for optimizing the time spent in a patch, the foraging gains per unit time, that is, the ratio of the two, are maximized. Many studies use optimization of the ratio or difference with context-specific appropriateness. It is recognized that the foraging strategies need to change according to what is limiting (Norberg 1977). For example, many studies recognize that maximizing the energy gain per unit time is different from maximizing the energy gain per unit energy spent (Schmid-Hempel et al. 1985, McNamara & Houston 1997, Charlton and Houston 2010). The optimum with or without considering resting energy consumption or time cost can be substantially different (Houston 1995, Houston & McNamara 2014). The need to
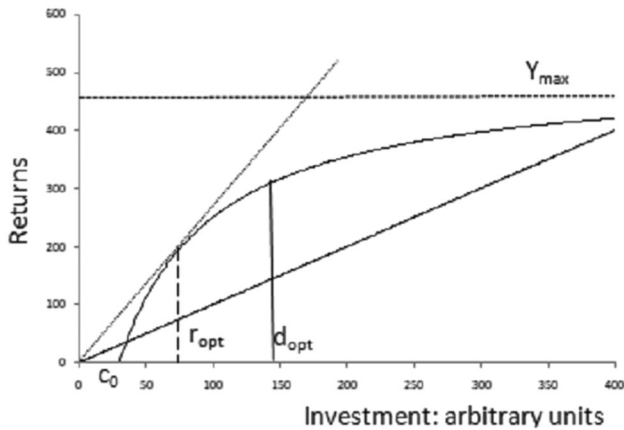
Evolution

Figure 1. Adopted from Watve et al. (2016). A conceptual diagram explaining ratio optimization and difference optimization: When the output follows the law of diminishing returns and there is an overhead cost (C_0), the inputs where the benefit-cost ratio is maximized is where the tangent drawn from the origin touches the curve. The benefit-cost difference is maximized where the vertical difference between the curve and the breakeven line is maximum or where the tangent to the curve becomes parallel to the breakeven line (Charnov 1976). For any profitable relationship, the ratio optimum is always on the left of the difference optimum. How much one should invest in a behavioral act depends upon whether ratio is being maximized or difference is being maximized.

distinguish between the net rate of gain, that is, gain minus expenditure, and the efficiency, that is, gain per unit expenditure, is also recognized and the conditions under which they differ or become equivalent are discussed in a context-specific way (Charlton & Houston 2010, Houston & McNamara 2014). A simpler explanation of when to maximize difference and when to maximize ratio was given by Watve et al. (2016) in the context of crop damage by wild animals. After a certain threshold, investing further in the current unit of investment will give a net gain or a rate of gain smaller than the average potential from other units and therefore investing into other units is better than further investing in the same unit (Fig. 1). This is parallel to the marginal value theorem (Charnov 1976) stated in the context of optimizing foraging time spent in a patch, except that we suggest two distinct ways of deciding the giving up point. Although the ratio or the difference is "maximized," the investment is "optimized," that is, on both sides of the optimum the ratio or difference declines, respectively. We use the words ratio optimum and difference optimum for these two points, respectively. The outcomes and the policy implications of ratio versus difference optimization can be substantially different.

Taking from the earlier context-specific models, we make a general case here to illustrate under what conditions the ratio or difference optimum applies, under what conditions the net rate

of gain and gain per unit expenditure are equivalent to the ratio and difference optima, and further how this simple rule gives additional clarity to many of the long-standing issues in behavioral ecology.

The Watve et al. (2016) Model

A baseline assumption of this model is a saturation curve, following the law of diminishing returns that is assumed in most optimization models in behavioral ecology (Charnov 1976, Parker and Maynard Smith 1990), economics (Brue 1993), and anthropology (Foley 1985). Conceptually, the differentiation between ratio and difference optimization can be used with other shapes of curves as well but we will use the saturation curve to develop a baseline model.

A difference optimization model maximizes the benefit per unit investment opportunity and therefore, when investment opportunities are limiting, this is the model of choice (Watve et al., 2016). On the other hand, the ratio model maximizes the benefit per unit investment and therefore when the investable amount is limiting, a ratio optimum should be used (Fig. 1). In reality, an individual can have multiple investable units and the net benefit of an individual is the sum of benefits from all invested units. There are two possible scenarios in which the total or lifetime benefit can be maximized.

If T is the total investable amount one has and N is the maximum number of identical units available for investment, one should choose the number of units n for investment and c the amount invested in each unit to get a return Y_c per unit such that $Y_c.n + T - n.c$ is maximized. The actual number of units invested in and the amount invested in each unit hold a constrained relationship such that $n \leq T/c$.

For $c \geq c_0$,

$$Y_c = \frac{Y_{max}(C - C_0)}{K + (C - C_0)}, \qquad (1)$$

while $c > c_0$ for ratio optimum $\frac{Y_{max}(C-C_0)}{K+(C-C_0)}/c$ is maximized and for difference optimum, $Y = \frac{Y_{max}(C-C_0)}{K+(C-C_0)} - c$ is maximized. By taking derivative dY/dc and finding c when the derivative becomes zero and the second derivative becomes negative, the optimum investment to maximize the ratio can be shown to be

$$c_{(ropt)} = c_0 + \sqrt{c_0 K}$$

or

$$cs_{(ropt)} = \sqrt{c_0 K}, \qquad (2)$$

where $cs = (c - c_0)$.
And the difference optimum to be

$$c_{(dopt)} = c_0 + \sqrt{K.Y_{max}} - K$$

or

$$cs_{(\mathrm{dopt})} = \sqrt{K.Y_{\max}} - K. \qquad (3)$$

From equations (2) and (3) it can be concluded that the ratio optimum cs is dependent on the overhead cost but not on $Y_{\max}$. In contrast, the difference optimum cs depends upon $Y_{\max}$ but not the overhead.

Limitations of the Watve et al. (2016) model lie in assuming that either T or N is clearly limiting. We show below that over a range of parameters, this is not true. Therefore, a generalizable model is needed that at specific conditions becomes equivalent to the ratio and difference models.

Equivalence to the Net Rate of Gain and Efficiency in Foraging Models

There is substantial theoretical as well as empirical work on foraging optimization (Pyke *et al.*, 1977, Stephens & Krebs 1987, Houston 1995, McNamara & Houston 1997, Charlton & Houston 2010, Houston & McNamara 2014). In fact, much of optimality theory developed in the context of foraging. In a typical honey bee model (Schmid-Hempel et al. 1985), for example, there is a hive to which the forager bees return with nectar load. The actual observation has been that often bees return to the hive with partially filled crops even when the source is far from depleted. This contradicts the models maximizing nectar delivery per unit time, that is, net rate of energy delivery (Schmid-Hempel et al. 1985). The partial crop filling is claimed to be better explained by the energetic costs of carrying nectar load, that is, energetic efficiency. However, if the partial crop filling was an all-time optimum, we would expect evolution of smaller crops. The existence of larger crop size implies that under certain set of conditions, larger loads would have been optimum. Optimizing the amount of nectar carried can be viewed as a ratio versus difference optimization problem. When the foraging patches are in excess, they need not maximize the nectar carried from one patch (Benedictis *et al.*, 1978). They need to maximize the nectar carried per unit time or unit energy expenditure, the two being correlated. On the other hand, when foraging patches are scares, they need to collect maximum nectar from a single patch. It is possible the crop size is optimized for difference optimum but when ratio optimum is appropriate, it is not necessary to carry the full crop load.

Some of the foraging models explicitly consider the net rate of gain (energy gain minus expenditure) and the efficiency (the ratio of energy gain and expenditure) separately. Houston and McNamara defined the net gain as $\gamma = (b - c)$, where b is the energy gain and c is the expenditure, and the efficiency is $q = b/c$. In their model, optimum foraging lies where $\frac{c + \frac{\varphi}{\alpha}}{\gamma}$ is min-

imized, ϕ being the fitness cost of time spent and α the fitness cost of metabolic expenditure. When ϕ is very small, that is, time needed per foraging bout is very small (indicating abundance of nectar patches), this optimum is equivalent to maximizing b/c, that is, ratio optimization of Watve et al. (2016) model. On the other hand, if time required to reach or explore one patch is very large so that ϕ/α is very large, c becomes negligible and maximizing $b - c$ is the appropriate strategy. Thus, the Houston and McNamara (2014) model can be viewed as a context-specific case of ratio versus difference optimization.

Constructing a Generalized Model
CURRENCY

A context-specific model involves currencies appropriate to the context such as time, effort, rewards, and so forth. In all biological examples, the ultimate currency is evolutionary fitness and all other variables such as time, energy, or risk need to be converted into the equivalence of evolutionary fitness. Mathematically, ratio of two different units is possible but not difference. Therefore, for applying the ratio/difference optimization principle, it is necessary that the costs and benefits are expressed in the same currency.

OPTIMIZING WHEN COMPLETE INFORMATION ABOUT THE INVESTABLE AMOUNT AND INVESTMENT OPPORTUNITIES IS AVAILABLE AT A TIME

If information about the investable amount T, the number of investment units N, and the parameters of the benefit curve is available, an optimum investment per unit that will maximize the total returns can be worked out starting with equation (1).

We choose c that maximizes $Y_c.n + T - n.c$ with the above constraint $n \leq N$. In some context, the residual investable amount, that is, $T - n.c$, can be relevant for the future and in certain other context, it may become irrelevant. For example, if the investment is being optimized for a given breeding season, the residual might be usable for the following seasons. However, if lifetime investment is being optimized, the residual has no relevance.

Using numerical simulations varying c, we examine at what value of c $Y_c.n + T - n.c$ is maximized. This is the optimum c that we plot as a function of variable N at constant T and variable T at constant N. In these curves (Fig. 2), the optimum investment per unit transits between a lower limit and an upper limit. It can be seen that at the lower limit, the ratio of Yc/c is maximum and at the upper limit the difference $Yc - c$ is maximum. Thus, the two limits of the optimum investment per unit correspond to the ratio optimum and difference optimum described earlier by Watve et al. (2016). When T is limiting but not N, the ratio
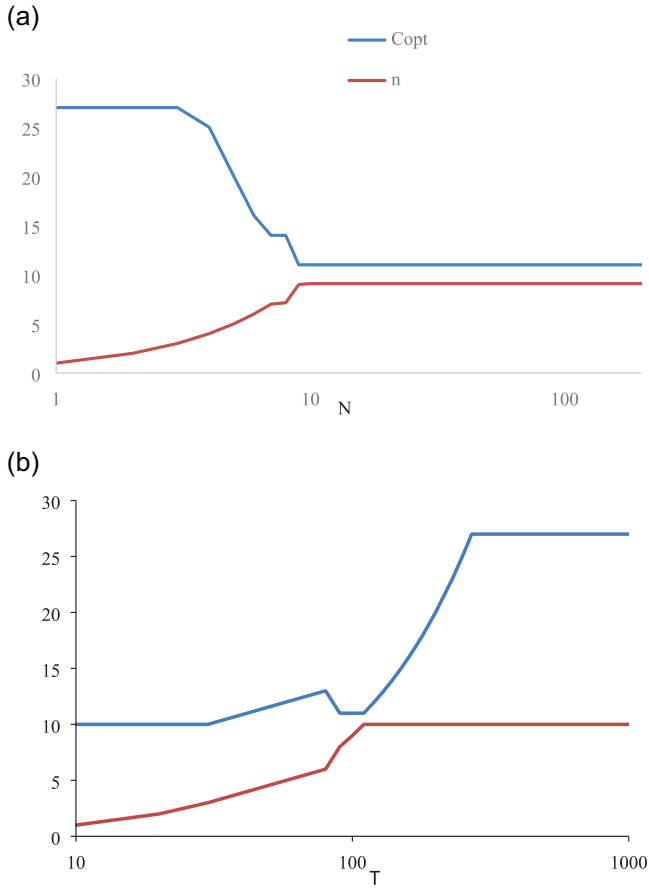
(a)

(b)

Figure 2. (A) The optimum investment per unit and the number of units invested with a fixed T and variable N. The optimum has two plateaus with a brief transition zone. When N is limiting, there is a higher plateau, and when N becomes so large that T becomes limiting, there is a lower plateau. Parameters used here are $Y_{max} = 100$, $K = 10$, $N = 1$–500, and $T = 100$. (b) Similarly, with constant N and variable T, a lower plateau can be seen when T is limiting and a higher plateau where N is limiting. There is a transition zone when neither T nor N is clearly limiting. Parameters used here are $Y_{max} = 100$, $K = 10$, $N = 10$, and $T = 1$–2000.

optimum gives maximum net returns summed over all investment units. On the other hand, when N is limiting but not T, difference optimum gives maximum net returns. It can be seen that if T is limiting, $T - n.c = 0$. On the other hand, if N is limiting, the residual amount $T - n.c$ cannot be invested anywhere. Therefore, in the two extreme conditions including or excluding $T - n.c$ in the optimization consideration does not change the optimum.

There is transient range when the true optimum lies between the two limiting optima, the trajectory of which may not be linear. Calculating an optimum in the transition zone needs prior information on all parameters. Earlier models did not consider this range.
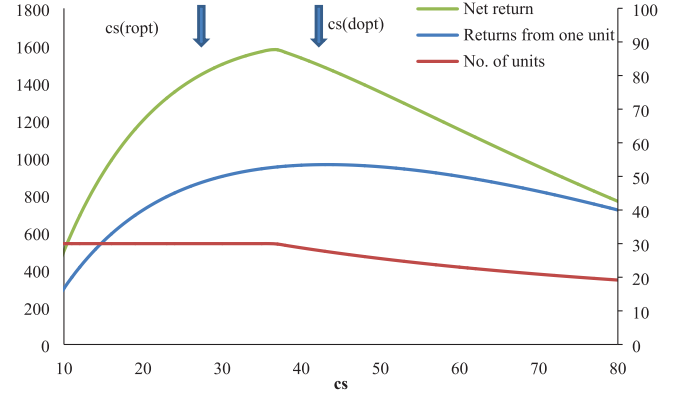

Figure 3. When $c_{(ropt)}.N < T < c_{(dopt)}.N$, that is, neither the investable amount nor the opportunities are clearly limiting, the optimum cs lies between the ratio optimum and difference optimum. Other parameters used here are $c_0 = 40$, $Y_{max} = 200$, $K = 20$, $N = 30$, and $T = 2300$.

When T is limiting, it can be shown that the net gain over the entire investment by ratio optimization is greater than that by difference optimization, because the ratio $\frac{Y_{(ropt)}}{c_{(ropt)}}$ is maximized:

$$\frac{T}{c_{(ropt)}} \left(Y_{(ropt)} - c_{(ropt)} \right) > \frac{T}{c_{(dopt)}} \left(Y_{(dopt)} - c_{(dopt)} \right),$$

$$T \left(\frac{Y_{(ropt)}}{c_{(ropt)}} - 1 \right) > T \left(\frac{Y_{(dopt)}}{c_{(dopt)}} - 1 \right).$$

On the other hand, when N is limiting, the net gain over the entire investment is greater by difference optimization because the difference $Y_{(dopt)} - c_{(dopt)}$ is maximized:

$$N \left(Y_{(ropt)} - c_{(ropt)} \right) < N \left(Y_{(dopt)} - c_{(dopt)} \right).$$

When $c_{(dopt)}.N < T$, the investable amount is not limiting but the number of investment units is. In this case, difference optimum should be used and when $c_{(ropt)}.N > T$, the investable amount becomes limiting and not the investment opportunities. In this case, ratio optimum should be used. However, because $c_{(dopt)} > c_{(ropt)}$, there will be a condition when

$$c_{(ropt)}.N < T < c_{(dopt)}.N.$$

This condition is the transition zone between the ratio and difference optimum as in Figure 2. When T is in this range and for a given cs, the net profit is

$$\left\{ \left[\frac{Y_{max}.cs}{K + cs} - c \right] . \text{Min} \left(N, \frac{T}{c} \right) \right\}.$$

cs at which the net profit is maximized will be the optimized cs. This transition can be jerky as the T/c becomes smaller than N. An example curve during transition from ratio to difference optimum is seen in Figure 3.

It can be easily seen that for finding the optimum in the transition zone knowing the parameters of the curve is not sufficient. One needs complete information about T and N simultaneously.

OPTIMIZING WITH INCOMPLETE INFORMATION

With real-life constraints, complete information about the lifetime investable amount or the number of investment opportunities available in lifetime is hardly ever available. These variables may also change with time, so extrapolative calculations are also unreliable. Therefore, most decisions are likely to be based on optimizing the investment in one unit at a time. With incomplete information, a simple rule of thumb would be to go by the ratio optimum or the difference optimum depending upon whether the perceived limiting factor is T or N. This is the most likely scenario in practice and therefore we expect most innate optimization methods as well as cognitive decisions to be based on either of the two limiting optima rather than on the precise calculation with complete information.

From equations (2) and (3), it can be seen that optimum cs for the ratio model increases with increasing overhead cost but is independent of Y_{max}. The optimum cs for the difference model is independent of the overheads, but varies with the square root of Y_{max}. These two distinctions can be used as differential testable predictions of the two models. Ratio optimizers should increase their investment when the overheads increase. Difference optimizers' optimum running cost should be independent of the overheads. A change in the maximum possible benefit, that is, Y_{max} on the other hand, will change a difference optimizer's investment in proportion to the square root of Y_{max}, whereas that of a ratio optimizer should remain unaltered.

We will see below how a strategic decision to use the ratio optimization or difference optimization influences the decision-making in human and nonhuman examples. We use examples from biology as well as from economics. The context, currency, and the mechanisms involved in optimizing may differ, but the optimization principles have close parallels.

Applications and Implications

The clarity about using ratio or difference optimization has many implications to behavioral ecology, evolution, economics, and policymaking. We intend to explore only a few such examples in which the ratio-difference concept is likely to bring better clarity and offer novel solutions to long-standing riddles. There is extensive background literature discussing all these issues and we neither intend to systematically review nor critique it but only suggest which new dimension or clarity can be added to these concepts by the ratio-difference optimization concept.

MALE AND FEMALE PARENTAL INVESTMENT

Sexual selection, sexual dimorphism, adult sex ratio, parental care, and the difference in male-female investment strategies are intertwined concepts and the causal relations between them have multiple interpretations (Trivers 1972, Clutton-Brock 1991, Kokko & Jennions 2008, Fromhage & Jennions 2016, Jennions and Fromhage 2017, Ratikainen et al. 2018, Clutton-Brock & Vincent 1991). By the fundamental biology of sex, females have greater investment in offspring than males mainly in terms of egg formation and maternal care wherever applicable. The males often have large investment in secondary sexual character, attractive display, and the risk associated. Inclusive of this, males' average total reproductive investment divided over all his offspring may not be less than the female average. Therefore, unlike classical assumption, the difference in male and female strategies is not explained by the total investment per offspring.

The ratio-difference optimization brings in much clarity in the complex dynamics of parental investment. Because the number of offspring a male can potentially have is not limiting, males are expected to be ratio optimizers. Females cannot increase the number of offspring by mating with multiple males and therefore they are limited by the investment opportunities and therefore are difference optimizers. Therefore, even if the total reproductive investment per offspring of males and females might turn out to be the same, their investment strategies need not be the same. The male's investment in secondary sexual character and display is an overhead cost in this model, but unlike our baseline model, males have a dual overhead cost. There is a preparative overhead necessary before access to females that is in the form of investment in size, strength, and/or display infrastructure. This component of investment does not increase with the number of females courted or mated. We call this type 1 overhead. The type 2 overhead is the additional cost to be paid per every female courted and consists of courtship and other behaviors targeted specifically and separately to individual females and/or individual offspring. Only type 2 overheads can be considered as c_0 of the model going by the model assumptions. Therefore, although the male's total investment may not always be lower than a female's, owing to the two stage overheads and use of ratio model, male's effective investment per offspring is more likely to be smaller than that of the female (Fig. 4).

If offspring survival is enhanced by paternal investment, the female should try to increase the type 2 overhead of the male by seeking more intensive courtship because in ratio optimization, the optimum cs increases with increase in c_0. A testable prediction of the model is that in species without the need for paternal care, type 1 overhead should dominate male displays but in species where some paternal inputs are needed, female choice and sexual selection will favor type 2 overheads, that is, active and individual oriented courtship over general display characters.
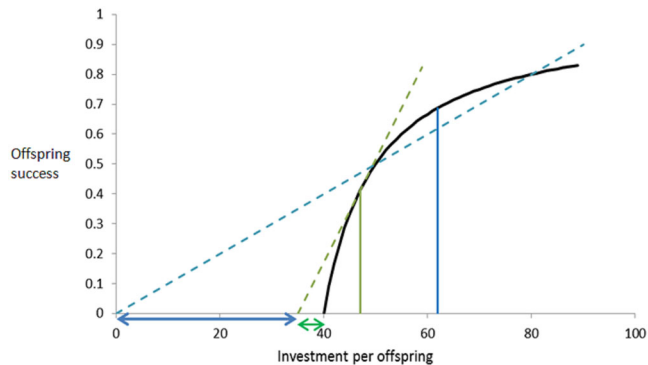
Figure 4. Difference between male and female investment in the offspring: We assume a case in which the net investment per offspring may be the same for males as well as females. We assume that the total overhead cost as well as the shape of the curve is the same. However, the nature of the overhead and the optimization models for males and females are different. The male overhead can be divided into the preparatory overhead (type 1—blue bar) and the courtship overhead (type 2—green bar). The former, once incurred, applies for all mating attempts and therefore does not figure in optimization of input per offspring. Second, males optimize the ratio. Females, on the other hand, have an overhead separately for every offspring and they optimize the difference. Therefore, male investment in offspring after fertilization is expected to be smaller than female investment, even when other factors remain the same.

Exercising a choice for type 2 overheads may result in an overhead cost for the female as well, but because in difference optimization, the optimum c_s is independent of the overhead, maternal investment per offspring will not be affected.

There are two types of factors affecting parental investment according to the ratio-difference optimization. A parent's optimum investment can change if the investment-returns curve changes. What type of change in the curve brings about increase or decrease in the investment would depend upon whether a ratio or difference optimization is being used? For example, greater predatory pressure can reduce offspring survival and thereby Y_{max} of the curve. We have seen that the ratio optimum is independent of Y_{max}, whereas the difference optimum is dependent. A testable prediction is that female investment per offspring would depend upon the presence or absence of predator, but male investment may not. The male investment, on the other hand, will increase if the type 2 overheads increase, but female investment will not. These principles can be further used to make species-specific testable predictions of the ratio-difference concept in the parental investment theory.

Our generalization that males are expected to be ratio optimizers and female's difference optimizers may change in specific contexts. If the number of surviving offspring is severely opportunity limited, even for a male, difference optimization may

become the model of choice and males would invest more in parental care (Benowitz *et al.*, 2013). Therefore, a parent's investment strategy may change either due to a change in the model itself or due to a change in the parameters of the curve. The two interact with each other and the nature of their interaction can also be modeled on the platform of the ratio-difference principle.

THE QUALITY-QUANTITY TRADE-OFF IN OFFSPRING

Because parents have limited resources, there is an inevitable trade-off between the investment per offspring and the number of offspring. Historically the trade-off was viewed by the theory of r and K selection based on logistic model of growth (MacArthur and Wilson 1967; Reznick *et al.*, 2002). The r and K selection theory came under criticism later and a more elaborate life-history optimization theory was proposed (Pianka 1970, Gadgil & Bossert 1970, Michod 1979, Kozlowski 1980, Charlesworth 1980, Stearns 1976, 1977, 1992, Derek 1993, Vitzthum, 2008). The life-history optimization also talks about optimum investment per offspring. It is recognized that selection for quality versus quantity of offspring is under a diversity of selective forces (Wilbur et al. 1974, Cassill 2019). The concept of ratio versus difference optimization can complement these theories and bring in greater clarity. Under certain contexts, the number of offspring is limited by parental investment and in certain other contexts by environmental opportunities. This is parallel to whether investable units, that is, number of offspring permitted by environmental opportunities, are limiting or the investable amount, that is, parental capacity, is limiting. When the environmental opportunities are in excess of what parental investment permits, the ratio optimum should decide the investment per offspring, and when the environmental opportunities are limiting the difference optimum should get selected.

It can be seen that under a set of assumptions, the ratio optimum is mathematically equivalent to r selection and difference optimum to K selection. If T is the lifetime investment in reproduction, c/T is the number of offspring. Taking $T = 1$, the birth rate b will be

$$b = \frac{1}{c}.$$

If Y is interpreted as survival probability of the offspring with $Y_{max} \leq 1$, $1 - Y$ is the death probability and $b(1 - y)$ the death rate. Therefore,

$$Y = \frac{b - d}{b} \text{ and } c = \frac{1}{b}.$$

Maximization of ratio $\frac{Y}{C_{(ropt)}}$ is equivalent to maximization of $\frac{b - d/b}{1/b} = b - d = r$.

Maximization of difference $Y - c_{(dopt)}$ is equivalent to maximization of

$$\frac{b - d}{b} - \frac{1}{b} = \frac{-d}{b}.$$

Maximizing $-d/b$ is maximizing b/d that is equivalent to K. Kozlowski (1980), Maynard Smith (1989), Charnov (1986), and Stearns (1992) agree that r selection maximizes $b - d$ and K selection maximizes b/d. Therefore, the ratio optimization is mathematically equivalent to r selection and difference optimization to K selection. However, ratio-difference optimization contributes to greater clarity in its real-life interpretation. The classical r and K selection concept talks about two alternative directions of selection but does not specify how far selection will drive along these directions, whereas the ratio versus difference optimum depicts two distinct optima. The cost–benefit optima focus on parental investment and a number of other aspects of density-dependent selection such as larval feeding rates and growth rates under density-dependent selection are not addressed.

OPTIMIZING THE PROPORTION OF NECTARLESS FLOWERS

It is known that in any species of flowering plants, a proportion of flowers contain nectar and others are empty (Simpson and Neff, 1981, Bell 1986,Thakar *et al.*, 2003, Anand *et al.*, 2007). There are multiple models of optimization of the proportion of the empty or "cheater" flowers (Bell 1986, Southwick 1987, Pyke 1991, Charnov and Orians, 2006, Bailey *et al.*, 2007; Morris *et al.*, 2010, Thakar *et al.*, 2003, Belsare *et al.*, 2009). The models so far have not explicitly considered alternative scenarios of whether the availability of pollinators is limiting or the number of flowers that can be made. If pollinators are limiting, the plants should follow a difference optimization model. In areas with pollinator abundance, they should follow ratio optimization. Thakar *et al* (2003) and Belsare *et al* (2009) used a difference model without explicitly defining the limiting factor. Incorporating the ratio-difference optimization in these models is likely to give better insights as well as make differential testable predictions that can drive novel experimental designs.

OPTIMIZING VIRAL BURST SIZE

For a virus infecting unicellular or multicellular hosts, the time for which a given cell is used for replication needs to be optimized. There can be a variety of rate-limiting steps in this process (Cummings *et al.*, 2012; Yin and Redovich, 2018). Initially, the virion population within a cell replicate exponentially as long as the virion number itself decides the rate of growth as seen in bacteriophage (Berngruber et al., 2013). At a later stage, however, some component of the cell's replication machinery can become limiting. Therefore, a virus has a choice to burst out early

before the machinery becomes rate limiting, to maximize the reproduction per unit time. However, by using a cell for a longer time, a virus can maximize replication per cell, but replication per unit time would be lower. Depending upon whether the constraint is time or the availability of cells, the length of the cycle and burst size would be optimized. For example, the influenza virus can invade a body only until the acquired immune response develops sufficiently to eliminate it (Chen *et al.*, 2018). Because time is the constraint, the virus needs to evolve a faster cycle with small burst size rather than compromising on the rate of growth for a longer life cycle with a larger burst size. The virus can afford to make suboptimum use of the cell capacity to support viral replication, because being a respiratory virus, finding another host is easier. In contrast, in the case of HIV, immune response is impaired on the one hand but on the other the mode of transmission is specialized and restrictive (Iwasaki, 2012), finding another host is more difficult. Therefore, influenza virus should be a ratio optimizer investing small time per cell and HIV should be a difference optimizer investing more time per cell and using the replication potential per cell fully. Compatible with the expectation is the estimated burst size of the slow growing HIV to be about 50,000 (Chen *et al.*, 2007) and that of the faster growing influenza virus to be 500–1000 virus particle per cell (Mahmoudabadi *et al.*, 2017).

PROTEIN STABILIZATION

For a cell, proteins need to be synthesized and then folded and maintained in the appropriate configuration (Cooper, 2000). The cell has an investment in protein synthesis and another set of investment in maintenance that includes chaperons (Bukau *et al.*, 2006; Tang *et al.*, 2008) and antioxidant mechanisms (Murray et al., 2018). In the worst case, the option of protein degradation and recycling of amino acids also exists. The investment in stabilizing a protein can be optimized either by the ratio model or the difference model. This strategic shift can be explained by ratio versus difference optimum. When protein synthesis is not limiting, the investment in protein maintenance is optimized by ratio. Therefore, there are greater chances of proteins misfolding and aggregation. In contrast when nutrient resources limit protein synthesis, there is greater investment in protein maintenance and recycling. This is likely to be the strategic reason for some of the beneficial effects of caloric restriction in minimizing pathologies associated with protein aggregation (Watve *et al.*, 2006, Baig*et al.*, 2014a, Matai *et al.*, 2019, Yang & Zhang 2020). A testable prediction of this model has actually been tested by Baig et al. (2014b), who showed that bacterial cells accumulate misfolded proteins when the external supply of nutrients is not limiting. On the other hand, when nutrient supply is limiting, there is greater investment in protein maintenance and recycling.

From the examples discussed, it can be seen that the ratio versus difference dichotomy can have implications for understanding the behavior of a variety of species or systems. The differentiation can address some long-standing paradoxes and conundrums, develop new insights into problems as well as stimulate new questions and novel experimental designs.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA ARCHIVING
xvtfd.

LITERATURE CITED
Anand, C., Umranikar, C., Shintre, P., Damle, A., Kale, J., Joshi, J. & Watve, M.G. (2007) Presence of two types of flowers with respect to nectar sugar in two gregariously flowering species. *Journal of Biosciences*, 32, 769–774.

Baig, U., Bhadbhade, B. & Watve, M. (2014a) Evolution of aging and death: what insights bacteria can provide. *Quarterly Review of Biology*, 89, 209–233.

Baig, U., Bhadbhade, J., Mariyam, D. & Watve, M. (2014b) Protein aggregation in *E. coli*: short term and long term effects of nutrient density. *Plos One*, 9, e107445.

Baig, U., Lokhande, L., Lalwani, P., Chawla, S. & Watve, M. (2019) Foraging theory and the propensity to be obese: an alternative to thrift. *Homo*, 70, 193–216.

Bailey, S.F., Hargreaves, A.L., Hechtenthal, S.D., Laird, R.A., Latty, T.M., Reid, T.G., Teucher, A.C. & Tindall, J.R. (2007) Empty flowers as a pollination-enhancement strategy. *Evol. Ecol. Res.*, 9, 1245–1262.

Bell, G. (1986) The evolution of empty flowers. *J TheorBiol*, 118, 253–258.

Belsare, P.V., Sriram, B. & Watve, M.G. (2009) The co-optimization of floral display and nectar reward. *Journal of biosciences*, 34(6), 963–967.

Benedictis, P.A.D., FB, G., Hainsworth, F.R., Pyke, G.H. & Wolf, L.L. (1978) Optimal meal size in hummingbirds. *American Naturalist*, 112, 301–316

Benowitz, K.M., Head, M.L., Williams, C.A., Moore, A.J. & Royle, N.J. (2013) Male age mediates reproductive investment and response to paternity assurance. *Proceedings of the Royal Society B: Biological Sciences*, 280(1764), 20131124.

Berngruber, T.W., Froissart, R., Choisy, M. & Gandon, S. (2013) Evolution of virulence in emerging epidemics. *PLoSPathog*, 9(3), e1003209. https://doi.org/10.1371/journal.ppat.1003209

Brue, S.L. (1993) Retrospectives: the law of diminishing returns. *Journal of Economic Perspectives*, 7(3), 185–192.

Budaev, S., Jørgensen, C., Mangel, M., Eliassen, S. & Giske, J. (2019) Decision-making from the animal perspective: bridging ecology and subjective cognition. *Frontiers in Ecology and Evolution*, 2019, 7, 164.

Bukau, B., Weissman, J. & Horwich, A. (2006) Molecular chaperones and protein quality control. *Cell*, 125(3): 443–451.

Cassill, D.L. (2019) Extending r/K selection with a maternal risk-management model that classifies animal species into divergent natural selection categories. *Science Reports*, 9, 6111.

Charlesworth, B. (1980) Evolution in age structured populations. Cambridge Univ. Press, Cambridge, U.K.

Charlton, N.L. & Houston, A.I. (2010) What currency do bumble bees maximize? *Plos One*, 5(8), e12186.

Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. *Theoretical population biology*, 9(2), 129–136.

Charnov, E.L. (1986) Life history evolution in a "recruitment population": why are adult mortality rates constant? *Oikos*, 47(2), 129–134.

Charnov, E. & Orians, G.H. 2006. Optimal foraging: some theoretical explorations. Ph.D. thesis, University of Washington, Seattle, WA.

Chen, H.Y. Di Mascio, M. Perelson, A.S., Ho, D.D. & Zhang, L. (2007) Determination of virus burst size in vivo using a single-cycle SIV in rhesus macaques. *Proceedings of the National Academy of Sciences of the United States of America*, 104(48), 19079–19084.

Chen, X., Liu, S., Goraya, M.U., Maarouf, M., Huang, S. & Chen, J.L. (2018) Host immune response to influenza A virus infection. *Frontiers in immunology*, 9, 320.

Clutton-Brock, T.H. & Vincent, A.C.J. 1991. Sexual selection and the potential reproductive rates of males and females. *Nature*, 351, 58–60.

Clutton-Brock, T.H. (1991) The evolution of parental care. Princeton Univ. Press, Princeton, NJ.

Cooper, G.M. (2000) The cell: a molecular approach. 2nd ed. Sinauer Associates, Sunderland, MA.

Cummings, K.W., Levy, D.N. & Wodarz, D. (2012) Increased burst size in multiply infected cells can alter basic virus dynamics. *Biology Direct*, 7, 16.

Derek, R.A. (1993) Evolution of life histories: theory and analysis. Springer, Berlin.

Doniol-Valcroze, T., Lesage, V., Giard, J., & Michaud, R. (2011) Optimal foraging theory predicts diving and feeding strategies of the largest marine predator. *Behavioral Ecology*, 22(4), 880–888.

Foley, R. (1985) Optimality theory in anthropology. *Man*, 20, 222–242.

Fromhage, L. & Jennions, M.D. (2016) Coevolution of parental investment and sexually selected traits drives sex-role divergence. *Nature communications*, 7(1), 1–11.

Gadgil, M. & Bossert, W.H. (1970) Life historical consequences of natural selection. *The American Naturalist*, 104(935), 1–24.

Ha, T. (2010) Optimality conditions for several types of efficient solutions of set-valued optimization problems. Pp. 305–324 *in* P. Pardalos, T. Rassias, and A. Khan, eds. Nonlinear analysis and variational problems. Springer, New York.

Houston, A.I. (1995) Energetic constraints and foraging efficiency, *Behavioral Ecology*, 6, 393–396.

Houston, A.I. & McNamara, J.M. (2014) Foraging currencies, metabolism and behavioural routines. *The Journal of animal ecology*, 83(1), 30–40.

Iwasaki, A. (2012) Innate immune recognition of HIV-1. *Immunity*, 37(3), 389–398.

Jennions, M.D. & Fromhage, L. (2017) Not all sex ratios are equal: the Fisher condition, parental care and sexual selection. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1729), 20160312.

Kokko, H., & Jennions, M.D. (2008) Parental investment, sexual selection and sex ratios. *Journal of evolutionary biology*, 21(4), 919–948.

Kozlowski, J. (1980) Density dependence, the logistic equation and r- and K-selection: a critique and an alternative approach. *Evolutionary theory*, 5, 89–101.

MacArthur, R.H. & Wilson, E.O. (1967) The theory of island biogeography. Princeton Univ. Press, Princeton, NJ.

Mahmoudabadi, G., Milo, R. & Phillips, R. (2017) Energetic cost of building a virus. *Proceedings of the National Academy of Sciences of the United States of America*, 114(22), E4324–E4333.

Matai, L., Sarkar, G.C., Chamoli, M., Malik, Y., Malik, Y., Kumar, S.S., Rautela, U., et al (2019) Dietary restriction improves proteostasis and increases life span through endoplasmic reticulum hormesis. *Proceedings of the National Academy of Sciences*, 116(35), 17383–17392.

Maynard, S.J. (1989) Evolutionary genetics. Oxford Univ. Press, Oxford, U.K.

McNamara, J.M. & Houston, AI. (1997) Currencies for foraging based on energetic gain. *Am Nat.*, 150(5), 603–17.

Michod, R.E. (1979) Evolution of life histories in response to age-specific mortality factors. *American Naturalist*, 113, 531–550.

Morris, W.F., Vázquez, D.P. & Chacoff, N.P. (2010) Benefit and cost curves for typical pollination mutualisms. *Ecology*, 91(5), 1276–1285.

Murray, D., Mirzayans, R. & McBride, W.H. (2018) Defenses against pro-oxidant forces—maintenance of cellular and genomic integrity and longevity. *Radiation research*, 190(4), 331–349.

Norberg, R. (1977) An ecological theory on foraging time and energetics and choice of optimal food-searching method. *Journal of Animal Ecology*, 46(2), 511–529.

Parker, G.A. & Maynard Smith, J. (1990) Optimality theory in evolutionary biology. *Nature*, 348(6296), 27–33.

Pianka, E. (1970) On r- and K-selection. *The American Naturalist*, 104(940), 592–597.

Pyke, G., Pulliam, H. & Charnov, E. (1977) Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology*, 52(2), 137–154

Pyke, G.H. (1991) What does it cost the plant to produce floral nectar? *Nature*, 350, 58–59.

Rahnev, D. & Denison, R.N. (2018) Suboptimality in perceptual decision making. *Behavioral and Brain Sciences*, 41, e223, 1–66.

Ramírez-Bautista, A., Balderas-Valdivia, C., Vitt, LJ. & Price, A.H. (2000) Reproductive ecology of the whiptail lizard *Cnemidophorus lineatissimus* (Squamata: Teiidae) in a tropical dry forest. *Copeia*, 2000(3), 712–722.

Ratikainen, I.I., Haaland, T.R. & Wright, J. (2018) Differential allocation of parental investment and the trade-off between size and number of offspring. *Proceedings of the Royal Society B: Biological Sciences*, 285(1884), 20181074.

Reznick, D., Bryant, M.J. & Bashey, F. (2002) r-and K-selection revisited: the role of population regulation in life-history evolution. *Ecology*, 83(6), 1509–1520.

Trivers, R. 1972. Parental investment and sexual selection. Pp. 136–179 *in* B. Campbell, ed. Sexual selection & the descent of man. Aldine de Gruyter, New York.

Schmid-Hempel, P., Kacelnik, A. & Houston, A. (1985) Honeybees maximize efficiency by not filling their crop. *Behavioral Ecology and Sociobiology*, 17(1), 61–66.

Simpson, B.B. & Neff, J.L. (1981) Floral rewards: alternatives to pollen and nectar. *Annals of the Missouri botanical Garden*, 68, 301–322.

Southwick, E. (1987) Photosynthate allocation to floral nectar: a neglected energy investment; *Ecology*, 65, 1775–1779

Stearns, S.C. (1976) Life history tactics: a review of the ideas. *Quarterly Review of Biology*, 51, 3–47.

Stearns, S.C. (1977) The evolution of life history traits. A critique of the theory and a review of the data. *Annual Review of Ecology and Systematics*, 8, 145–171.

Stearns, S.C. (1992) The evolution of life histories. Oxford Univ. Press, Oxford, U.K.

Stephens, D.W. & Krebs, J. (1987) Foraging theory. 1st ed. Princeton Univ. Press, Princeton, NJ.

Tang, Y., Chang, H., Chakraborty, K., Hartl, F.U. & Hayer-Hartl, M. (2008) Essential role of the chaperonin folding compartment in vivo. *The EMBO Journal*, 27, 1458–1468.

Thakar, J.D., Kunte, K., Chauhan, A.K., Watve, A.V. & Watve, M.G. (2003) Nectarless flowers: ecological correlates and evolutionary stability. *Oecologia*, 136(4), 565–570.

Vitzthum, V.J. (2008) Evolutionary models of women's reproductive functioning. *Annual Review of Anthropology*, 37, 53–73.

Watve, M., Bayani, A. & Ghosh, S. (2016) Crop damage by wild herbivores: insights obtained from optimization models. *Current Science*, 111, 861–867.

Watve, M., Parab, S., Jogdand, P. & Keni, S. (2006) Aging may be a conditional strategic choice and not an inevitable outcome for bacteria. *Proceedings of the National Academy of Sciences*, 103(40), 14831–14835.

Wilbur, H.M., Tinkle, D.W. & Collins, J.P. (1974) Environmental certainty, trophic level, and resource availability in life history evolution. *American Naturalist*, 108, 805–816.

Yang, Y. & Zhang, L. (2020) The effects of caloric restriction and its mimetics in Alzheimer's disease through autophagy pathways, *Food Funct*, 11(2), 1211–1224

Yin, J. & Redovich, J. (2018) Kinetic modeling of virus growth in cells. *Microbiology and Molecular Biology Reviews*, 82, e00066-17.