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A general framework for modelling trade-offs in adaptive behaviour

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ABSTRACT

An animal's behaviour can influence many variables, such as its energy reserves, its risk of injury or mortality, and its rate of reproduction. To identify the optimal action in a given situation, these various effects can be compared in the common currency of reproductive value. While this idea has been widely used to study trade-offs between pairs of variables, e.g. between energy gain *versus* survival, here we present a unified framework that makes explicit how these various trade-offs fit together. This unification covers a wide range of biological phenomena, highlighting similarities in their logical structure and helping to identify knowledge gaps. To fill one such gap, we present a new model of foraging under the risk of predation and damage accumulation. We conclude by discussing the use and limitations of state-dependent optimisation theory in predicting biological observations.

Key words: life-history, foraging, reserves, condition, predation, state-dependent optimisation, dynamic programming.

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I. INTRODUCTION

A central idea in evolutionary biology is that natural selection favours phenotypic strategies that maximise an individual organism's expected lifetime reproductive success (fitness) (Zimmer & Emlen, 2016; Futuyma & Kirkpatrick, 2018).

To make testable predictions on this basis one needs methods for identifying strategies that meet this criterion. Such methods face the challenge that the range of possible strategies can be large. Especially in the evolution of state-dependent behaviour, every action taken by an animal may affect its available options at later times. For example, if an

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animal builds up fat reserves in autumn, this creates the option to live off these reserves in winter without needing to forage or migrate. Whether an action is good (i.e. adaptive) or bad thus cannot be evaluated in isolation: it depends both on the action's consequences and on the animal's anticipated future actions in a world shaped by those consequences (León, 1976; Freeman & McFarland, 1982; Mangel & Clark, 1986; McNamara & Houston, 1986, 1994). However, if we take as given what strategy an individual will pursue in the future, a useful short-term criterion for judging adaptive behaviour becomes available: behavioural options in the present can then be compared by evaluating their consequences in the currency of reproductive value (Williams, 1966). Reproductive value measures a focal individual's expected contribution, from the present until the end of its life, to the population's future gene pool. This contribution depends on the individual's state; for example its size, energy reserves, or parasite load. How state changes over time depends on the individual's actions. This means that the effect of an action on future reproductive success can be quantified through its effect on the state of the individual. In this way, state variables provide a mechanistic link between an action's immediate and delayed consequences.

We focus on two state variables: by x_1 we denote an individual's stored energy (e.g. fat reserves); and by x_2 we denote its structural integrity ('condition') that may become damaged e.g. during hard work or dangerous activities. For an overview of notation, see Table 1. Other state variables (e.g. body size, information, location, present activity) are conceptually analogous but are omitted here for clarity.

A major strength of the concept of reproductive value is that it provides a common currency for comparing qualitatively different outcomes (McNamara & Houston, 1986), which makes it uniquely useful for studying trade-offs. Although many trade-offs have been studied with this methodology (including cases with more than one state variable, e.g. Mangel & Clark, 1986; Lucas & Walter, 1991; Cichon, 2001; Mangel & Munch, 2005; Satterthwaite *et al.*, 2009; Brodin, Nilsson & Nord, 2017; King, Kirkwood & Shanley, 2017), no unified framework has yet been presented for describing how these various trade-offs all fit together. By filling this gap, here we aim to highlight similarities in the logical structure of seemingly disparate biological questions and to identify aspects deserving further investigation.

We express an organism's reproductive value $V(x_1, x_2, t)$ as a function of its state variables (x_1, x_2) and time (t). Time is relevant especially in seasonal environments, where fat reserves are more crucial in times of food shortage. We use a continuous-time framework where an action's consequences are expressed as instantaneous rates of change. For an individual choosing behavioural option u , these consequences include mortality [at rate $M(u)$], reproduction [at rate $R(u)$], and changes of energy and condition [at rates $\gamma_1(u)$ and $\gamma_2(u)$, respectively]. By summarising how these various consequences affect the individual's expected (current and future) reproductive success, we obtain a currency that measures

Table 1. Notation.

Symbol	Meaning
$b(u)$	Energy expenditure rate
B	Benefit of performing a social act
C	Cost of performing a social act
$D(u)$	Rate of build-up of damage
e	Energy content of food item
$H(u; x_1, x_2, t)$	Rate of increase in reproductive value under action u when in state (x_1, x_2) at time t
$L(t, s)$	Probability that an individual survives until time s given that it is alive at time t
$m(t)$	Mortality rate at time t on an individual's life trajectory
$M(u)$	Mortality rate as a function of u
$r(t)$	Reproductive rate at time t on an individual's life trajectory
$R(u)$	Reproductive rate as a function of u
t	Time
u	Behavioural option
$u^*(x_1, x_2, t)$	Optimal action u when in state (x_1, x_2) at time t
$v(t)$	Reproductive value at time t on an individual's life trajectory
$v'(t)$	Rate of change of reproductive value
$V(x_1, x_2, t)$	Reproductive value as a function of x_1, x_2, t (abbreviated to V for simplicity)
x_1	Energy reserves
x_2	Body condition
$\alpha_1(u)$	Food detection rate when performing action u
γ_1	Rate of increase in x_1
γ_2	Rate of increase in x_2
τ_1	Mean duration of interrupted period

the rate of increase in reproductive value H under action u when in state (x_1, x_2) at time t :

$$H(u; x_1, x_2, t) = \gamma_1(u) \frac{\partial V}{\partial x_1} + \gamma_2(u) \frac{\partial V}{\partial x_2} - M(u)V + R(u). \quad (1)$$

Here V is the individual's current reproductive value, i.e. $V = V(x_1, x_2, t)$. Similarly, the partial derivatives of V are evaluated at (x_1, x_2, t) . Behaviour, u , controls four variables, each corresponding to one of the four terms on the right-hand side of Equation (1), and each contributing to the rate of change of V . The first two terms in Equation (1) are weighted by partial derivatives that translate physiological changes in energy reserves and body condition into changes in V . The third term is weighted by V to account for the value of life lost when mortality strikes. The fourth term has no weighting because it directly concerns the 'present reproduction' component of V . The optimal action in state (x_1, x_2) at time t , $u^*(x_1, x_2, t)$, satisfies $H(u^*(x_1, x_2, t); x_1, x_2, t) = \max_u H(u; x_1, x_2, t)$ i.e. it maximises the rate of increase of V . Typically this optimal action varies with state and time, although in what follows, for ease of notation we will abbreviate $H(u, x_1, x_2, t)$ to $H(u)$ and $u^*(x_1, x_2, t)$ to u^* .

Whereas mortality is a stochastic effect, changes of state are here modelled as deterministic for simplicity. To relax

this simplification, Equation (1) must be suitably modified. We will illustrate in Section II how this can be done.

Because V can be increased no further once the optimal strategy is already in use, there is then no net increase in V over time. Formally,

$$0 = \frac{\partial V}{\partial t} + \max_u H(u). \quad (2)$$

This equation, known as the Hamilton–Jacobi–Bellman equation (Sieniutycz, 2007; Weber, 2011; Lewis, Vrabie & Syrmos, 2012), has been used to investigate the action of natural selection in a variety of contexts (e.g. Taylor *et al.*, 1974; León, 1976; Ludwig & Rowe, 1990; Sasaki & Iwasa, 1991; Thygesen *et al.*, 2016; Pike, McNamara & Houston, 2018; Thygesen & Patterson, 2019). The term $\frac{\partial V}{\partial t}$ accounts for the passage of time; it describes how V would change with time if state were held constant. Another way of putting this is that adaptive behaviour will not increase V insofar as its effects, including the effects on mortality and reproduction, are already anticipated in the calculation of V . A heuristic derivation of this equation is given in the online Supporting Information, Appendix S1.

If Equation (2) holds for every possible state and time, then the behavioural strategy maximises reproductive success across the individual's lifetime. We note, however, that the task of instantaneous maximisation at a particular time relies on knowing V at that time, and since V depends on the strategy used at all future times, this requires knowledge of the solution of Equation (2) at all future times (*cf.* Freeman & McFarland, 1982). The latter proviso is not as restrictive as it sounds, however, as it can be met by identifying the optimal strategy successively in the inverse direction of time. Pontryagin's maximum principle works in this manner (Jacobs, 1974; Perrin & Sibly, 1993; Weber, 2011; Lewis *et al.*, 2012) but is impractical for many situations. Instead it is simpler to have actions taken on a discrete time grid, and then use a technique called dynamic programming (Bellman, 1957; Houston & McNamara, 1999; Clark & Mangel, 2000). For the discrete-time analogue of Equation (2), see Appendix S2.

Two points deserve special emphasis: (i) we can always view a dynamic problem as a case of instantaneous maximisation, but one that involves a term that depends on the future: V in our case. (ii) Although maximisation of the right-hand side of Equation (2) for all states and times maximises lifetime reproductive success, this does not mean that the instantaneous rate of reproduction is maximised at any point in time; it may be better to limit reproduction now in order to reproduce more later. Even if there is currently no reproduction and an organism is just concerned with food acquisition, it may not be optimal to maximise immediate food gain. For example, rather than continuing to forage on an already-depleted food patch, it may be better to interrupt feeding to move to a better food patch (Charnov, 1976).

We can also track how reproductive value changes over time for an individual. Suppose that $x_1(t)$ and $x_2(t)$ are the

two state variables for the individual as a function of time t . We can think of $(x_1(t), x_2(t))$ as defining a trajectory for the individual in state space. We can then follow various quantities along this trajectory. Let $v(t) = V(x_1(t), x_2(t), t)$ denote the reproductive value of the individual at time t , given it is still alive. We write $v(t)$ as a function of t here to establish t as an index by which we can refer to points in the individual's life trajectory. This does not imply that t is causally relevant in itself. We note that

$$v(t) = \int_t^\infty L(t, s)r(s)ds, \quad (3)$$

where $L(t, s)$ is the probability that the individual survives until time s , given that it is alive at time t , and $r(s)$ is the rate of reproduction at time s . From this (see Appendix S3) we infer that the rate of change of this quantity is given by

$$v'(t) = m(t)v(t) - r(t), \quad (4)$$

where $m(t)$ is the rate of mortality at time t (Freeman & McFarland, 1982). This formula emphasises that reproductive value is concerned with future prospects: if during some non-reproductive time period of fixed duration there is a risk of mortality and this mortality is avoided, then $v(t)$ increases because the probability of surviving until reproduction increases; if during a reproductive period of fixed duration there is no mortality risk then $v(t)$ decreases with time, since as t increases there is less reproduction in the future.

Equation (4) gives the change in reproductive value as an individual is followed along its life-history trajectory. We can illustrate this by considering a gravid female that is approaching reproduction. The equation shows that over time the female's reproductive value will only increase over her pregnancy if she is subject to a mortality risk. Her reproductive value is not increasing explicitly as a result of a change in her state, since the change of state is already anticipated in the definition of reproductive value. By contrast, if we compare the reproductive value of the gravid female with a non-gravid female at the same time of year, then the gravid female will tend to have a higher reproductive value for two reasons. One is that the non-gravid female may not have time to breed this year, the other is that she may die before she can become gravid.

II. TRADE-OFFS

By considering all pairwise combinations of terms in Equation (1), we can identify six trade-offs (Table 2). We comment on each of these in turn, both from a theoretical and empirical perspective. We begin with the trade-off between reserves and survival, which is the context in which

Table 2. The six trade-offs implicit in Equation (1), with biological examples.

	Mortality	Reproduction	Condition
Reserves	(1) foraging under predation risk	(2) rut-induced hypophagia; nuptial feeding; provisioning of offspring	(3) prey choice in the face of defence mechanisms or infection risk
Condition	(4) combating disease under predation risk; autotomy	(5) mating contests; injurious mating; sexually transmitted diseases; general costs of reproduction	
Mortality		(6) fatal mating contests; courting and mating under predation risk; sexual cannibalism	

Caraco (1979) first introduced the idea of marginal rates of substitution into behavioural ecology. These rates are useful for studying trade-offs because they answer the question: to compensate for a small change in one factor, by how much must another factor be adjusted so that the animal is indifferent to the overall change (Caraco, 1979; Brown, 1988)? In the following subsections, we present simplified versions of Equation (1) in which some terms are dropped because they are assumed to be constant in u . For example, Equation (5) applies when there is neither reproduction nor change in condition (x_2).

(1) Reserves *versus* mortality

$$H(u) = \gamma_1(u) \frac{\partial V}{\partial x_1} - M(u) V. \quad (5)$$

Foraging is often associated with a mortality risk, e.g. because it increases the likelihood of encountering predators. An animal's foraging decisions should therefore depend on how urgently it needs food, and on the predation risk faced when foraging or not. The optimal action under a food *versus* predation trade-off is the value of u that maximises the right-hand side of Equation (5). There, the term $\gamma_1(u)$ is the rate of increase of reserves with time and $\frac{\partial V}{\partial x_1}$ is the rate of increase of future reproductive success with reserves. The product of the two terms is the rate at which future reproductive success increases with time as a result of food gain. The term $M(u)$ is the rate of mortality and V is the potential loss in future reproductive success that will occur in the event of the individual's death. The product of these two terms thus is the rate of expected loss of future reproductive success as a result of predation. It is optimal to maximise the net rate of increase in future reproductive success [Houston & McNamara, 1989, 2014; Houston, McNamara & Hutchinson, 1993; Brown & Kotler, 2004; Nevai, Waite & Passino, 2007; Thygesen & Mazuryn, 2022; for a similar trade-off between growth and survival, see Ludwig & Rowe (1990); Skalski & Gilliam, 2002].

Given a range of actions which differ in predation risk and energy intake, some actions should never be chosen. For

example, an action should not be chosen if an alternative action offers the same rate of energy gain at a lower predation risk; or if the alternative offers a higher energy gain at the same predation risk. Figure 1 illustrates the set of 'admissible' actions.

It can be seen from Equation (5) that lines of constant H in (γ_1, M) space are straight lines with slope $\frac{\partial V}{\partial x_1} / V$. For example if γ_1 (which is scaled by $\frac{\partial V}{\partial x_1}$) were increased by one unit, then a compensating increase in M (which is scaled by V) would have to be of magnitude $\frac{\partial V}{\partial x_1} / V$. Thus when there is a trade-off between food and predation risk, the ratio $\frac{\partial V}{\partial x_1} / V$ specifies how much the energy intake rate would need to increase to compensate for an increase in mortality rate so that the animal is indifferent to the overall change. The ratio is called the marginal rate of substitution of energy for life (McNamara & Houston, 1986, 1994; Brown, 1988, 1992; Houston & McNamara, 1989; Brown & Kotler, 2004). Figure 1 illustrates how the best action depends on this marginal rate of substitution. An animal with high energy reserves (Fig. 1A) is liable to have a lower marginal rate of substitution of energy for life than an animal with low reserves (Fig. 1B). This is because the value of energy ($\partial V / \partial x_1$) will tend to be lower and the value of the animal's life (V) will be higher. The animal should therefore take fewer risks to obtain food when reserves are high than when reserves are low (compare Fig. 1A,B) (Mangel & Clark, 1986; McNamara & Houston, 1986, 1990; Brown, 1988; Houston & McNamara, 1988; McNamara, 1990). Clark (1994) calls the observation that increasing V results in less risky behaviour the 'asset protection principle'. In line with this principle, a comparative study by Moran *et al.* (2021) found that animals given low-quality food were more likely to take risks.

A small bird in winter typically faces a food *versus* predation trade-off. Models predict that a bird should take fewer risks (for example by resting rather than foraging) when its fat reserves are high (Lima, 1986; McNamara & Houston, 1990; McNamara *et al.*, 2005). The setting in winter is relevant here because it rules out reproduction as an alternative route of investment, thus simplifying the situation to a pure survival task. A small bird in winter faces uncertainty in the food supply, so that Equation (5) needs to be modified. The appropriate

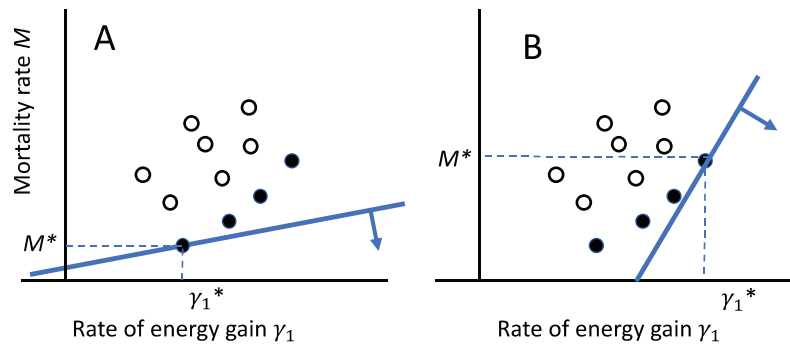


Fig. 1. The relation between mortality rate M due to predation and rate of energy gain γ_1 . (A) Each point represents a behavioural option, as characterised by γ_1 and M (Gilliam & Fraser, 1987). The bold line is an isocline connecting hypothetical combinations of M and γ_1 that would yield the same fitness. The isocline's slope is the marginal rate of substitution of energy for life $((\partial V/\partial x_1)/V)$, where x_1 is energy reserves and V is reproductive value. It characterises a focal individual's disposition to trade off safety for energy. The arrow shows the direction in which fitness increases. The optimal action has energy gain rate γ_1^* and predation rate M^* . (B) The same set of actions as seen by a low-resource individual, whose greater need for energy (quantified by $\partial V/\partial x_1$) and/or lower reproductive value manifests in a steeper isocline. The individual should accept a higher predation risk in order to gain energy rapidly. Options that do not lie on the point cloud's lower-right edge are represented as open circles. Such options are not admissible (i.e. should not be chosen by any individual) because there is always an unequivocally superior alternative. In economic terms, these options are not on the Pareto front (Miettinen, 1998).

modification depends on how stochasticity operates. To illustrate, suppose that a bird with energy reserves x_1 that takes action u finds food items of energy content e at rate $\alpha_1(u)$, and uses energy at rate $b(u)$. Then Equation (5) is modified to

$$H(u) = \alpha_1(u)[V(x_1 + e, t) - V(x_1, t)] - b(u) \frac{\partial V}{\partial x_1} - M(u)V. \quad (6)$$

Variants of this equation have been used by McNamara & Houston (1989) and Mangel (1992). The expression in square brackets represents the gain of reproductive value when a food item is found, so the whole first term on the right-hand side of Equation (6) represents the expected rate of gain of reproductive value associated with the chosen action. Other forms of stochasticity can be incorporated in a similar way. For example, if foraging can be interrupted by bad weather forcing the bird to rest, then Equation (5) must be modified to include a term proportional to the rate of this occurrence, summarising the event's consequences. This form of stochasticity is illustrated in Section II.3.

(2) Reserves versus reproduction

$$H(u) = \gamma_1(u) \frac{\partial V}{\partial x_1} + R(u). \quad (7)$$

A trade-off between acquiring reserves and reproduction may arise as a result of a limited time budget, if seeking

food and seeking matings are mutually exclusive activities. This has been suggested to explain rut-induced hypophagia (i.e. reduced foraging during the mating season) in male bighorn sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*); here the time spent feeding, although reduced in absolute terms, remained constant relative to the time spent resting (Pelletier, Mainguy & Côté, 2009). Moose (*Alces alces*) bulls, by contrast, often give up feeding altogether during the rut, despite spending about half of their time inactive rather than engaged in social behaviour (Miquelle, 1990). This suggests that rut-induced hypophagia in moose, rather than merely reflecting a time constraint, may reflect physiological constraints that render it inefficient to switch between mating and feeding in the short term.

In species where mating requires a food item being passed from male to female (nuptial feeding), the male has to decide between eating the food or offering it to his mate [e.g. in European bee-eaters *Merops apiaster* (Avery *et al.*, 1988); scorpion flies *Panorpa cognata* (Engqvist, 2007)]. Eating the food may be preferable if the male can thus avoid starvation, allowing him to reproduce later; passing on the food may be preferable otherwise.

As Fig. 2 illustrates, a trade-off between feeding and reproduction may lead to specialisation in one or the other activity at different life-history stages. For example, males in certain web-building spiders (Herberstein *et al.*, 2005; Segoli, Harari & Lubin, 2006), and mayflies (order Ephemeroptera) of both sexes, do not feed after reaching adulthood, the latter having vestigial mouthparts and an air-filled digestive system that enhances flight performance (Gillott, 2005). This performance advantage points to interference between simultaneous activities as the ecological driver of specialisation. A web-building spider male's

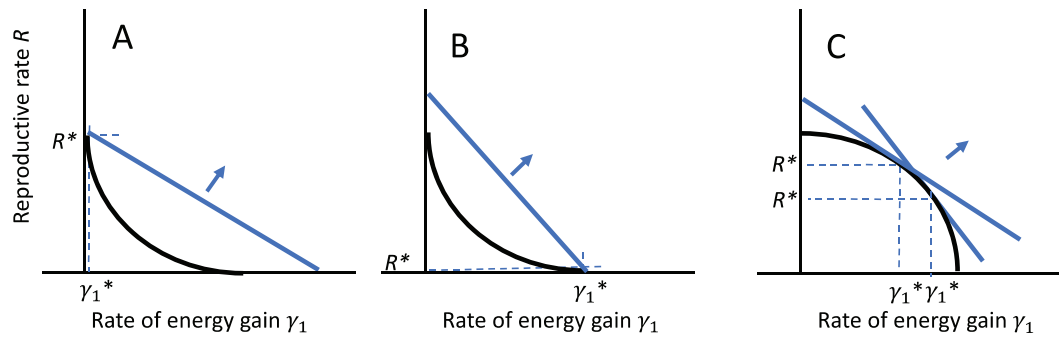


Fig. 2. The relation between reproductive rate R and rate of energy gain γ_1 . (A) The bold black line describes the set of behavioural options, spanning the continuum between focussing exclusively on either reproduction or feeding. Its convex shape reflects the assumption that reproducing and feeding simultaneously is inefficient. The bold blue line is an isocline with slope $-\partial V/\partial x_1$, where x_1 is energy reserves and V is reproductive value, which connects combinations of reproduction and feeding rate that would yield equal fitness. The arrow shows the direction in which fitness increases. For the individual shown, it is optimal to focus exclusively on reproduction, at rate R^* and energy gain rate $\gamma_1^* = 0$. (B) The same set of behavioural options as seen by a low-resource individual whose greater need for energy makes it optimal to prioritise energy gain instead of reproduction. (C) A concave option set, reflecting the assumption that simultaneous reproduction and feeding is more efficient than either activity alone. Two isoclines are shown (bold blue lines), corresponding to different individuals with different reserve levels. As the isocline becomes steeper, individuals gradually place increasing emphasis on feeding.

stationary feeding style seems difficult to combine with mate-searching, which may result in a convex trade-off curve (Fig. 2A,B). By contrast, if a ground-hunting spider's mate-search performance is synergistically improved through frequent replenishment of energy, this may result in a concave trade-off curve (Fig. 2C).

Note that in these invertebrate examples, in parallel with the above case of hypophagia in moose, limited behavioural flexibility may reflect a strategy that keeps to a minimum the presumably costly switching between activities. Finally, the provisioning of offspring is another way of investing in reproduction that may be traded off against a parent's reserves (Kacelnik & Cuthill, 1990). Over a longer timescale, this is related to the distinction between using stored energy to cover the cost of a breeding attempt (capital breeding) as opposed to gaining energy during the attempt (income breeding) (Stephens *et al.*, 2009).

(3) Reserves versus condition

$$H(u) = \gamma_1(u) \frac{\partial V}{\partial x_1} + \gamma_2(u) \frac{\partial V}{\partial x_2}. \quad (8)$$

Animals can often acquire food, i.e. replenish their reserves, at a risk of damaging their body. For example, predators must face morphological, chemical, or behavioural defences of their prey (Mukherjee & Heithaus, 2013). The corresponding equation, Equation (8), was introduced by Houston & McNamara (1999, their eqn 4.12; see also Houston & McNamara, 2014). This trade-off may explain why oystercatchers (*Haematopus ostralegus*) prefer to feed on small

cockles, although large cockles would yield a higher instantaneous intake rate. Because large cockles have thick shells, feeding on them is associated with a risk of beak damage, which would reduce the bird's foraging efficiency in the long run (Rutten *et al.*, 2006). Moreover, large cockles carry a greater load of harmful parasites (Norris, 1999), so that their nutritional value may not be worth the associated damage. The latter aspect is analogous to the risk of parasite infection incurred by grazing sheep (*Ovis aries*) on faeces-contaminated sward. Unsurprisingly, sheep avoid contaminated sward unless they are hungry and alternative feeding options are much less nutritionally profitable (Hutchings, Kyriazakis & Gordon, 2001). Similar to the oystercatchers mentioned above, shore crabs (*Cancer magister*, *Carcinus maenas*) prefer to feed on smaller clams that do not maximise energy intake but limit the risk of claw damage (Juanes & Hartwick, 1990; Smallegange & Van Der Meer, 2003). Damage – and indeed the complete loss of limbs and other appendages – commonly occurs in species capable of autotomy, the voluntary casting off of body parts in situations of danger (Embets, Escalante & Bateman, 2019). Such danger may often arise in a context of foraging, thus contributing to the trade-off between reserves and condition. Autotomy can have various negative consequences (compared to surviving with all body parts), including reduced foraging efficiency, reduced mating success, and increased vulnerability to attack (Juanes & Smith, 1995; Cooper, Pérez-Mellado & Vitt, 2004; Maginnis, 2006). Van Den Heuvel *et al.* (2017) explore a model in which damage decreases the ability to feed and increases mortality. Yet another form of damage is induced by defensive plant toxins contained in food (McArthur *et al.*, 2012; Bedoya-Pérez *et al.*, 2014).

The various forms of damage mentioned above differ in the extent to which repair is possible.

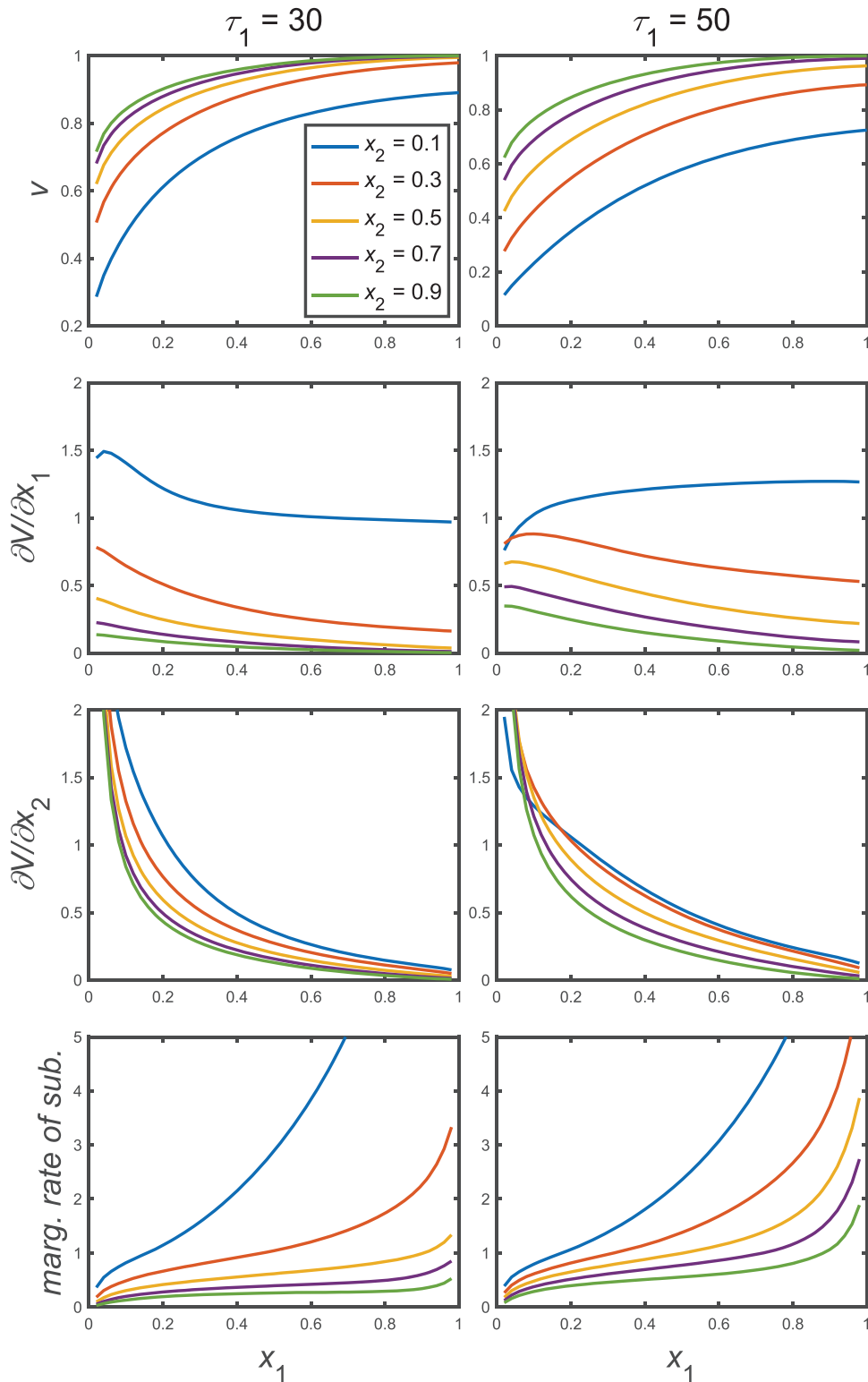


Fig. 3. The dependence of reproductive value (V) of an uninterrupted animal on reserves x_1 and condition x_2 , in the model outlined in Appendix S4. Results for two mean durations of an interrupted period, τ_1 , are shown. Top row: the dependence of V on reserves, x_1 , and condition, x_2 . Second row: the marginal rate at which reproductive value increases with reserves, $\partial V / \partial x_1$. Third row: the marginal rate at which reproductive value increases with condition, $\partial V / \partial x_2$. Bottom row: the marginal rate of substitution of reserves for condition, $\frac{\partial V_1}{\partial x_1} / \frac{\partial V_1}{\partial x_2}$. See Appendix S6 for Fortran code used to produce this figure.

We now look at a model in which high foraging effort increases damage, but damage can be repaired if the animal reduces its effort or rests. The rate of mortality increases as damage increases. Stochasticity arises because foraging is subject to interruptions. Details of this model are given in Appendix S4. Figure 3 compares the properties of reproductive value in two cases that differ in how long interruptions to foraging last. Reproductive value V increases with both reserves and condition in both cases (Fig. 3, top row). However, the increase with reserves (x_1) may occur at an increasing or decreasing rate (Fig. 3, second row). Intuitively, this occurs because individuals with critically low resources benefit less from feeding if they face a substantial risk of starving anyway; and because high-resource individuals experience diminishing returns through satiation. For similar reasons, an individual with critically low condition may benefit less from increasing its condition, at least if its resources are so low that they will take time to recover (Fig. 3, third row, blue line located below the other lines on left edge of right panel). At any given level of x_1 and x_2 , the marginal rate of substitution of reserves for condition $\frac{dV_1}{dx_1} / \frac{dV_1}{dx_2}$ (Fig. 3, bottom row) increases with x_1 , and more strongly so with increasing x_1 and decreasing x_2 .

(4) Condition versus mortality

$$H(u) = \gamma_2(u) \frac{\partial V}{\partial x_2} - M(u)V. \quad (9)$$

When faced with adverse external conditions, animals commonly mount a ‘stress response’ (Selye, 1976) involving both behavioural and physiological changes (Sapolsky & Wingfield, 2003; Taborsky *et al.*, 2021). McNamara & Buchanan (2005) have investigated theoretically an animal’s optimal resource allocation in the face of a transient stressful event such as the presence of a predator. In their model, resources can be allocated either to avoiding the predator, thus enhancing short-term survival, or to bodily maintenance, thus avoiding the build-up of damage and enhancing long-term survival (provided the predator does not kill the animal). Their analysis produced a counter-intuitive result: predator-induced mortality could be reduced when the predator was more dangerous, reflecting a shift in the priorities of the prey species.

In animals capable of autotomy (see Section II.3), a slightly different form of this trade-off occurs; lizards may cast off their tails (Cooper, 2003), and arthropods one or more of their limbs (Fleming, Muller & Bateman, 2007), to escape a predator, thus saving their lives in the short term at a cost of damaging their body. Because autotomy involves a discontinuous change in x_2 , it calls for a modification of Equation (9) analogous to Equation (6).

(5) Condition versus reproduction

$$H(u) = \gamma_2(u) \frac{\partial V}{\partial x_2} + R(u). \quad (10)$$

Sources of damage in a context of reproduction include injurious fights for mating opportunities (Riechert, 1998), injuries inflicted during copulation by the male on the female (Crudginton & Siva-Jothy, 2000; Morrow & Arnqvist, 2003) or *vice versa* (Sakaluk *et al.*, 2004; Fromhage & Schneider, 2006), sexually transmitted diseases (Kokko *et al.*, 2002; Knell & Webberley, 2004), and various kinds of physical (e.g. wear and tear) and physiological (e.g. DNA and cellular protein) deterioration associated with the production of (and care of) offspring. In kestrels (*Falco tinnunculus*), caring for experimentally enlarged broods induced excess mortality during the following winter (Daan, Deerenberg & Dijkstra, 1996). While the mechanism responsible remained unclear, the observed delay between cause and effects appeared more consistent with physiological damage (e.g. impaired immune system, degenerative cell destruction) than merely depleted energy reserves. Following a mechanical injury, reproduction is commonly reduced in favour of regeneration in a wide range of species (Rennolds & Bely, 2023). Accounting for a trade-off between damage and reproduction can dramatically change the predictions of life-history models: using this approach, McNamara *et al.* (2009) showed that the classical prediction that organisms should invest increasingly in reproduction as they approach the end of their life (e.g. Clutton-Brock, 1984) is reversed under broad conditions.

(6) Mortality versus reproduction

$$H(u) = -M(u)V + R(u). \quad (11)$$

Death may often strike in a context of reproduction (Magnhagen, 1991), e.g. because courtship signals attract predators, because copulating pairs and gravid females are easy prey (but see Gwynne, 1989), and because the need to feed a hungry brood induces parents to adopt riskier foraging options (Pike *et al.*, 2018). Fatal fights for mating opportunities (Enquist & Leimar, 1990), and sexually cannibalistic females (Tuni *et al.*, 2020), add further to the death toll of reproduction. Where risk varies across contexts, some situations are more suitable for reproduction than others. Males in the spider *Nephila fenestrata* are relatively safe from sexual cannibalism if approaching a feeding female, which is what they prefer to do (Fromhage & Schneider, 2005). Male rock lizards (*Lacerta monticola*), too, appear to trade-off mating opportunities against predation risk: following a simulated predator attack, they re-emerged more quickly from their

refuge when mating opportunities seemed good (Martin, Lopez & Cooper, 2003). Because both components of Equation (11) may depend on state, the same is likely to be true of the optimal policy; senescent individuals may avoid activities that require a highly functioning body to mitigate risk [i.e. for which $M(u)$ is forbiddingly high with weakened sense organs and muscles]; or they may make a terminal reproductive investment because they have little to lose [low V (Gadgil & Bossert, 1970; but see McNamara *et al.*, 2009)].

(7) Trade-offs involving more than two factors

Although listed above as a study of the trade-off between condition and reproduction (see Section II.5), it is worth noting that McNamara *et al.* (2009) considered that instantaneous mortality, too, can vary between behavioural options. Thus, by addressing a three-way trade-off between damage, reproduction, and instantaneous death, McNamara *et al.* (2009) already went some way towards the unification presented herein. They showed that, under the assumption that the individual will die once its accumulated level of damage reaches some threshold, the optimal policy should maximise

$$H(u) = \frac{R(u) - M(u)V}{D(u)}, \quad (12)$$

where $D(u)$ is the rate of build up of damage, i.e. the negative of the rate of change of condition, $(-\gamma_2(u))$ when performing action u . We rederive this equation in Appendix S5. Intuitively, it means that individuals should pace their build-up of damage in such a way that for every increment, they attain the highest possible gain of (current and future) net reproduction.

(8) Time-independent trade-offs

In non-seasonal environments, it may be the case that neither an individual's options nor the consequences of its actions change over time. If so, then the corresponding optimal policy will also be time independent. In this special case, it is possible to find a simplified currency which must be maximised by an optimal strategy (Appendix S5). Depending on the trade-off under consideration, this currency can be the rate of energy gain per mortality risk, $\gamma_1(u)/M(u)$ (Werner & Gilliam, 1984), or the rate of reproduction per mortality risk, $R(u)/M(u)$ (Houston & McNamara, 1986).

III. DISCUSSION

We used a standard approach to finding optimal behaviour (the Hamilton–Jacobi–Bellman equation) to develop a framework for analysing trade-offs. Apart from offering a methodology for modelling a wide range of phenomena, some insights about biology follow directly from our

equations. In the case of the familiar trade-off between energy reserves *versus* predation, Equation (5) shows that the animal should maximise its intake rate γ_1 regardless of predation risk, provided that predation does not depend on foraging behaviour [$M(u)$ is constant]. With hindsight this may not seem surprising, but it counters the intuition expressed by Dawkins (1995, p. 28–30) that maximisation of intake rate is necessarily a short-sighted strategy that is suboptimal in the long run. The key point is whether the animal can trade off energy reserves against predation. If it cannot, then predation does not matter for optimal foraging behaviour. Here and elsewhere in this paper, we use the phrase ‘the animal should do X’ to indicate what behaviour would be optimal from a standpoint of adaptive behaviour. Such optimality arguments are a useful source of predictions, even though real animals do not always behave optimally.

Some of the trade-offs we have discussed are dealt with in life-history theory (Taylor *et al.*, 1974; León, 1976; Stearns, 1992; Roff, 2002). Traditional life-history theory is based on classifying individuals by age, with trade-offs characterised by age-dependent relationships between mortality and reproduction. At each age, an individual's reproductive effort determines its survival and reproduction (Schaffer, 1983). These life-history models typically involve annual decisions [but see McNamara *et al.* (2004, 2008) for weekly decisions], whereas we have focused on behavioural decisions on a finer timescale. The fact that decisions during one period ‘carry over’ (O'Connor *et al.*, 2014) to later periods is easy to capture by working with state (Barta *et al.*, 2008).

Many life-history models take size to be a state variable when modelling the allocation of resources to growth or reproduction (e.g. Kozłowski, 1992; Perrin & Sibly, 1993; Kozłowski & Teriokhin, 1999). To incorporate senescence, such models may assume *a priori* that mortality is age dependent (Kozłowski & Teriokhin, 1999). An alternative approach is to take condition to be a state variable (McNamara & Houston, 1996; McNamara *et al.*, 2009) and let senescence emerge as a consequence of imperfect repair; this is the disposable soma principle (Kirkwood, 1979; Abrams & Ludwig, 1995; Shanley & Kirkwood, 2000; King *et al.*, 2017; Van Den Heuvel *et al.*, 2017). Cichon & Kozłowski (2000), Cichon (2001) and Mangel & Munch (2005) analyse models that include both size and condition. It is worth noting that, although the disposable soma theory was originally formulated in terms of the allocation of energy to different body functions, a trade-off between maintenance (i.e. condition) *versus* reproduction need not be mediated by energy (see Section II.5). Thus, energy limitation is not a crucial assumption of the disposable soma theory (*contra* Lidsky & Andino, 2022).

In general, the solution to a dynamic optimisation problem can be given in the form of instantaneous maximisation [using dynamic programming or Pontryagin's Maximum Principle (Jacobs, 1974; Perrin & Sibly, 1993; Weber, 2011; Lewis *et al.*, 2012)]. This is well known in life-history theory, but although McFarland (1977) drew attention to it at the

behavioural level, it is not always understood. For example, Abrams (1991, p. 1250) dismisses Equation (5) on the grounds that it is ‘... based on the apparently unwarranted assertion that an organism should maximise its instantaneous rate of increase of fitness. This strategy is equally non-adaptive for animals as the seldom-used human strategy of maximising speed at every instant during a long-distance race’. Abrams’ spurious argument is instructive: the application of our approach to a race does not say that it is optimal to instantaneously maximise speed. Instead, the runner should instantaneously maximise the rate of increase in the value function, and this does not usually involve the maximisation of speed because there are trade-offs. For example, in the model of Keller (1974), an increase in speed increases oxygen consumption, which will force the runner to slow down later on. A more detailed physiological model using Pontryagin’s Maximum Principle is analysed by Cook *et al.* (2023). Similarly, foraging involves a trade-off between a positive effect – it increases energy and hence increases V , and a negative effect – it risks death. As a result, the optimal foraging intensity [given by Equation (5)] does not necessarily maximise energy gain in the short term.

The instantaneous maximisation envisaged in our approach depends on the future through V . We can find V from assuming that future decisions are optimal or by assuming the future has a particular form – e.g. the repeated choice of a specified option [this can be thought of as a fixed background (McNamara & Houston, 1989; Houston & McNamara, 1999)]. Thus after the focal decision, we could assume that if undamaged the animal gains energy at a fixed rate until some time T ; thus, long-term damage could be represented as lower rate of gain. Optimising over the future gives us a global optimum, whereas if the future is fixed, we get a constrained optimum (Houston & McNamara, 1985; McNamara & Houston, 1986). We emphasise that V is not a fixed property of an individual; it depends on the environment (see Fig. 3).

Although in general immediate maximization of a suitable quantity as a means of finding optimal behaviour should take the future into account, we have shown that, when V is independent of t , it can be optimal to maximise a simple currency that does not involve the future. Perhaps the best-known example is that of minimising mortality rate divided by growth rate when faced with an energy *versus* predation trade-off (Gilliam, 1982; Werner & Gilliam, 1984). This currency was derived by Gilliam (1982) in the case of an organism that has to reach a fixed size before it can reproduce; if the animal is gaining energy but not growing then the analogous currency to be minimised is mortality rate divided by gain rate. Neither currency is general [for further work on these currencies see Ludwig & Rowe (1990), Leonardsson (1991), Rowe & Ludwig (1991), Giske & Aksnes (1992), Houston *et al.* (1993) and Clark (1994)].

Mukherjee & Heithaus (2013) offer a framework for understanding the costs and benefits of foraging on dangerous prey. Although they review evidence that such prey might injure or kill a predator, their approach does not

include injury (i.e. damage) as a state variable. Instead they follow Berger-Tal *et al.* (2009) in treating injury like predation: ‘Hunting dangerous prey ... may lead to a wide range of costs – from none at all to death – that may occur with different probabilities that foragers may be able to assess. This is similar to making trade-offs between foraging opportunities and reducing predation risk’. (Mukherjee & Heithaus, 2013, p. 557). In other words, Mukherjee & Heithaus (2013) view hunting dangerous prey as an example of reserves *versus* predation (Section II.1). By contrast, the full equation for this case involves all terms in Equation (1) except R (Houston & McNamara 1999, eqn A4.1.2). More generally, whenever we are initially unsure about what trade-offs are relevant in a given biological context, our Equation (1) may provide a useful starting point. By starting with Equation (1) and eliminating from it irrelevant terms one by one, we may reduce the risk of overlooking something.

In his analysis of optimal patch use when food contains toxins, Schmidt (2000) uses a model with two state variables, energy and level of toxin. His equation contains the marginal value of energy and toxin, but the level of toxin has no effect on mortality during the period in question. Furthermore, the optimal solution is obtained using Lagrange multipliers which essentially ignores changes in state during the foraging period (see Houston & McNamara, 1999, section 6.9).

Freeman & McFarland (1982, eqn 34) used an equation similar to our Equation (1) to represent what they call a ‘cardinal measure of motivation’ (p. 43), whose terms are anticipated effects of activity u (on reproduction, mortality, etc.) that feed into the motivation for performing u . An animal behaves optimally if it always maximises H , so H can be seen as a common currency based on pleasure (Cabanac, 1992). Freeman & McFarland (1982) suggest that it would be optimal to pursue each activity to the point where all motivations are equally strong. In the simple contexts that they (and we) consider, such a system will jam or make frequent switches between activities (i.e. it will dither; Houston & Sumida, 1985) which is likely to be inefficient. A more detailed account would include spatial location or the activity currently being performed as part of the state. This would make it possible to represent the cost of switching from one activity to another. Mechanistic (‘motivational’) ways to reduce the frequency of switching could be based on positive feedback (Houston & Sumida, 1985) or inhibition (Marshall *et al.*, 2015).

Up to this point, our framework rests on the idea that natural selection tends to favour strategies that confer high lifetime reproductive success. However, because helping among relatives is an alternative mechanism by which individuals can propagate their genes, in general we expect organisms to adopt strategies that maximise their inclusive rather than personal fitness (Hamilton, 1964). In practice this means that actions should satisfy a time- and state-dependent version of Hamilton’s rule $\rho B > C$, where B is the action’s benefit (increase in reproductive value) conferred on a relative (with relatedness coefficient ρ) and C is the cost to the focal individual’s own reproductive value (McNamara,

Houston & Webb, 1994). This leads to a modified version of Equation (1)

$$\mathcal{J}(u) = \sum_i \rho_i H_i(u), \quad (13)$$

where the summation is over all relatives i with which the focal individual interacts (including the focal individual itself, for which relatedness $\rho_i = 1$; cf. Equation 35 in Freeman & McFarland, 1982). $\mathcal{J}(u)$ is analogous to $H(u)$ in Equation (1), but goes beyond it in that it captures not only a focal individual's rate of increase in reproductive value, but also the corresponding rates of its relatives. As before, u signifies only the focal individual's behaviour; the strategies of relatives are taken as fixed for the purposes of the maximisation. Individuals may differ in their $H_i(u)$, i.e. in how they are affected by the focal individual's behaviour. For example, a behaviour may increase a relative's reproduction at the expense of the focal individual's own reproduction. Over the whole population the $\mathcal{J}(u)$ need not sum to unity, since descent in the sense of sharing the same genes is not mutually exclusive (Freeman & McFarland, 1982).

Provided that a high level of within-colony cooperation is achieved, a social insect colony can be viewed as an individual (Seeley, 1997; Hölldobler & Wilson, 2009), with state variables such as energy, protein and number of workers (Schmid-Hempel, Winston & Ydenberg, 1993). A worker bee's foraging behaviour might control the rate at which it brings nectar to the colony and its mortality rate (Houston, Schmid-Hempel & Kacelnik, 1988), so that foraging influences both the energy reserves and the number of workers. This means that foragers may be able to increase colony energy at the cost of a decrease in colony 'condition'.

Here we have aimed to present simple and abstract models that illuminate the role of trade-offs in a general way. To give a more realistic account of particular species, models can incorporate taxon-specific information about physiological mechanisms. For example, such models of salmonid life histories could predict specific responses to environmental change, and also shed light on general phenomena such as genetic thresholds and genotype-by-environment interactions (Mangel & Satterthwaite, 2008; Satterthwaite *et al.*, 2009). Pecquerie *et al.* (2011) present an alternative approach. They use Dynamic Energy Budget theory (Sousa *et al.*, 2010), which does not assume that life histories are optimal, to explore variation between species of Pacific salmon.

A model's realism may often be increased by including additional state variables. Real animals acquire multiple kinds of nutrients, and incur multiple kinds of damage, all of which might be tracked separately. In addition to the conceptual and technical advantages of simplicity, however, there is also a biological reason for not going too far in that direction. The more detailed the description of a decision context, the fewer instances matching the description will have occurred during evolutionary history. In the limit, every situation is unique; but natural selection obviously cannot shape specialised responses for unique circumstances.

Instead, in practice we expect animals to use simple rules that work well across broad classes of circumstances (McNamara & Houston, 2009), called 'rules of thumb' in behavioural ecology and 'heuristics' in psychology (Hutchinson & Gigerenzer, 2005). Rules of thumb were originally proposed as simple solutions to complex foraging problems. Subsequent work in this tradition has covered additional topics (e.g. egg-laying in female parasitoids; Wajnberg, 2006), and has linked decisions to physiological states such as hunger (Higginson *et al.*, 2018). More generally, models of emotional state suggest a plausible mechanism by which behavioural rules can be implemented (Giske *et al.*, 2013, 2014), including in ways that involve expectations about the future (Budaev *et al.*, 2019; Håkonsrud Jensen *et al.*, 2021). Extending this approach to issues of animal welfare (Budaev *et al.*, 2020) suggests intriguing links to the evolution of consciousness (Birch, Ginsburg & Jablonka, 2020).

IV. CONCLUSIONS

- (1) Whether or not an animal's behaviour is adaptive cannot be evaluated without considering the animal's future behaviour. If this behaviour is known then alternative actions can be compared by evaluating their consequences in the currency of reproductive value, and the optimal action can be identified as the one which instantaneously maximises reproductive value. Intuitively, this means that an animal following the optimal strategy should at all times act so as to maximise the net rate of increase of its future reproductive success.
- (2) An action may have delayed consequences for survival and reproduction, mediated by state variables such as the level of reserves. An optimal strategy must therefore take changes in state variables into account.
- (3) We distinguish six pairwise trade-offs involving reproduction, mortality, body reserves and body condition. While these are often studied in isolation, we emphasise here that they may all occur simultaneously, and can be expressed in the same equation.
- (4) Pairwise trade-offs can be characterised in terms of their marginal rates of substitution, which quantify the relative value of small changes in each variable. For example, the marginal rate of substitution of energy for life (Caraco, 1979; Brown, 1988) makes it possible to compare the value of gaining energy with the cost of being killed. Similar conversion factors occur in the other trade-offs, e.g. reserves for condition, condition for mortality, etc.
- (5) Including condition as a state variable can radically change the predictions of life-history models, from elevated reproduction towards the end of life ('terminal investment') to gradual reproductive senescence as a consequence of imperfect repair (McNamara *et al.*, 2009). On a shorter time-scale, damage also makes explicit a reason other than predation why foragers should not always maximise their net rate of energy gain.

(6) We show that, when time *per se* does not affect reproductive value, it can be optimal to maximise a simplified currency such as the rate of energy gain per mortality risk (Werner & Gilliam, 1984) or the rate of reproduction per mortality risk (Houston & McNamara, 1986).

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VII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. The dynamic programming equation.

Appendix S2. The discrete-time dynamic programming equation.

Appendix S3. Change along a trajectory.

Appendix S4. Reserve and damage model.

Appendix S5. Currencies when there is no explicit time dependence.

Appendix S6. Fortran code used to produce Fig. 3.

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