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# The starvation–predation trade-off shapes the strategic use of protein for energy during fasting



Andrew D. Higginson<sup>a,\*</sup>, John M. McNamara<sup>b</sup>, Alasdair I. Houston<sup>a</sup>

<sup>a</sup> School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

<sup>b</sup> School of Mathematics, University of Bristol, University Walk, Bristol BS8 1TW, UK

## HIGHLIGHTS

- We model the optimal proportion of energy from protein catabolism during a period without food.
- Find quantitative agreement with observations on lean and obese penguins and rats.
- Animals have not evolved to maximise their starvation resistance.
- The risk of predation affects use of protein catabolism when starving.

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## ABSTRACT

The primary function of lipid storage by animals is as an energy source for surviving periods without food. However, muscle and organ protein can be metabolised for energy, and empirical studies have shown that the onset of protein metabolism begins before the exhaustion of lipid reserves. Since protein tissues are important for reasons other than resisting starvation, the adaptive basis for this early onset is unclear. Here, we report the results of a model of the optimal proportion of energy to obtain from protein catabolism during a period without food of unpredictable duration. We assume either that the animal aims only to maximise the duration of survival or that it also has to take account of its future reproductive success given its state when the food supply recommences. In the latter case we find impressive quantitative agreement with observations on lean and obese penguins and rats. Analysis shows that this agreement breaks down if predation risk is insignificant, protein in the form of muscle is ineffective against predation, or there is no benefit to conserving lipid (e.g. for reproduction). This result implies that animals have not evolved to maximise their starvation resistance because doing so would leave them vulnerable when an interruption ends. Our model allows us to make several specific predictions concerning the relationship between the ecological pressures on animals and their starvation survival strategies.

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## 1. Introduction

Animal adaptations to environments in which it is not always possible to find food include the storage of lipids and the catabolism of proteins as an energy source (McCue, 2010; Wells, 2010). Although lipid storage has several functions, the primary function is to compensate for a shortfall in energy intake relative to energy requirements (Pond, 1998). Shortfalls may occur on multiple time-scales, such as from minutes to many weeks, and may occur even when the animal does find food. However, the best studied are those

situations of outright famine, where energy intake is zero and the animal is fasting.

Observations on various species of fasting mammals and birds suggest a phylogenetically conserved strategy of resistance to death from starvation (McCue, 2010). Across taxa, changes in the strategic use of resources during fasting lead to characterisation of the fasting pattern as consisting of three phases (Goodman et al., 1980; Le Maho et al., 1976, 1981; Robin et al., 1987). During Phase I energetic requirements are met by the catabolism of glycogen. Phase II starts when glycogen is exhausted and so energy is primarily generated from the oxidation of lipids; proteins are partially spared. Phase III is characterised by the increase in the catabolism of protein. It would seem reasonable to suppose that animals should avoid catabolising bodily protein, especially skeletal muscle, and it is therefore surprising

\* Corresponding author. Tel.: +44 117 928 7478.

E-mail address: [adhigginson@gmail.com](mailto:adhigginson@gmail.com) (A.D. Higginson).

that the onset of protein catabolism in Phase II typically precedes the exhaustion of lipid reserves. There may be selective pressure to conserve lipid stores, especially deep-lying adipose tissues (Pond, 1992, 2002) but seemingly less important stores, especially peripheral subcutaneous tissues, are still present during Phase III (Wells, 2010). These tissues may have other functions, such as fuelling the immune system (Pond, 1992, 2002) or the thermal insulation provided by blubber in marine mammals (Pond, 1998). In addition to these influences extrinsic to the animal it might be adaptive to catabolise protein as a fuel early in the fasting period because muscle is highly active tissue, using around 10 times more energy than lipid stores for an active animal (Berthold et al., 2003; Kvist and Lindström, 2001; Lindström and Kvist, 1995; Lindström et al., 2000; Scott and Evans, 1992; Scott et al., 1996). Hence, the early catabolism of muscle may reduce the rate of energy use and so prolong the duration of the fast that can be sustained.

Although the three phases described above have been observed in many animals, there is variation among taxa in the strategies that animals use in terms of protein catabolism (McCue, 2010; Pond, 1998). Much variation is due to requirements for thermogenesis (Lee et al., 2012), but this does not explain broad patterns across taxa, or individual variation. With regards the former, it seems that protein provides more energy during starvation in mammals than in birds (Jenni and Jenni-Eiermann, 1998). Within species, the use of protein during fasting is influenced by the state of the animal in the early stages of the fast, where an inverse relationship is found between the use of protein and the proportion of the wet body mass that is lipid (adiposity). For animals with high adiposity (> 30%), the catabolism of protein is minimal. By contrast, for animals with low adiposity (< 15%), protein use can be initially very high. This was first noted a century ago (Voit, 1901), and has been repeatedly confirmed since (Cherel et al., 1992; Dunn et al., 1982; Goodman et al., 1980; Harlow and Buskirk, 1991; Lindgard et al., 1992). These differences provide a base from which to understand the causes and consequences of variation among the strategies that have evolved.

The approaches to starvation survival strategies outlined above typically aim to describe the effect of lipid levels and metabolic costs in order to understand mechanisms. There has been less attention paid to understanding the selective pressures on the starvation strategy of different animals. One most obvious constraint is that reproductive value – the animal's expected future reproductive success (McNamara and Houston, 1986) – is likely to depend on its state at the end of the fast. A potentially important influence on the reproductive value of the animal at the end of the fast is its agility and strength, especially when it starts to forage to restore its condition. A reduction in skeletal muscle without a corresponding decrease in the mass of other tissues is likely to reduce the athletic ability of the animal, which may both increase vulnerability to predators and decrease the ability of the animal to catch its prey (Dietz et al., 2007). Also, catabolism of gut tissue (Ruthrauff et al., 2013) will reduce food processing ability, thereby reducing the speed of recovery (Dietz and Piersma, 2007). Hence, we might expect animals to preserve muscle and gut tissue in order that mortality rate is not especially high when foraging recommences. On the other hand, animals might also need to preserve energetic stores if interruptions to the food supply sometimes occur one after another, meaning there is a trade-off between surviving the current interruption and surviving any possible future interruption.

In this paper, we present a theoretical approach that provides functional explanations for starvation strategies by the use of a state-dependent framework, where the strategy is partly determined by the reproductive value consequences of the animal's state when fasting ends. We find excellent agreement with detailed observations on mammals and birds, suggesting that

our assumptions of selective pressures are realistic. This work therefore demonstrates the potential for variation in the magnitude of different quantifiable intrinsic and ecological pressures, such as predation rate whilst foraging and the likelihood of further interruptions, to underlie between- and within-species differences in the strategies used to resist starvation.

## 2. A model of fasting

The model uses a state-dependent dynamic programming approach (Clark and Mangel, 2000; Houston and McNamara, 1999) to find the optimal use of protein for energy during a period without feeding. A similar, simpler approach has been used successfully to predict the strategy of Northern elephant seal pups (Noren and Mangel, 2004). The model is parameterised from empirical data presented in a descriptive proximate model (Caloin, 2004). Our model represents an advance on these studies because we include benefits of protein other than as an alternative energy source in order to elucidate the selective pressures that have shaped this strategy.

We characterise the animal as consisting of skeleton ( $S$ ), basal muscle that cannot be metabolised without death occurring ( $B$ ), lipid stores ( $L$ ) and extra muscle and organs that can be metabolised ( $P$ ).  $S$  and  $B$  are fixed whilst  $L$  and  $P$  change over the starvation period. We assume that during an interruption to the food supply the animal cannot feed and must use lipid and/or protein stores to meet the energetic and protein requirements. The decision made by the animal is what proportion of energetic requirements to obtain from catabolising protein ( $\delta$ ). The rate of energy use ( $E_{USE}$ ) and the rate of protein use ( $P_{USE}$ ) required to stay alive are

$$E_{USE} = \theta_L L + \theta_P (P + B) \quad (1a)$$

$$P_{USE} = \psi (P + B) \quad (1b)$$

where  $\theta_L$  and  $\theta_P$  control the rate of energy use by lipid and protein tissues respectively and  $\psi$  controls the rate of the use of protein in maintaining organs, such as in muscle repair. If the animal has insufficient protein or lipid to meet these requirements then the animal dies. We assume that the protein requirements of lipid stores are negligible and can be ignored (J. Wells, personal communication), and that  $\theta_L$ ,  $\theta_P$ , and  $\psi$  are constant over the starvation period. That is, a unit of protein or lipid uses resources at a constant rate regardless of the amounts of each component. In order to calculate body components as proportions of observable wet body mass, we assume that adipose tissue and bones contain no water but proteinaceous tissue (muscles and organs) are associated with  $3 \times$  their mass of water (Caloin, 2004). Thus total wet body mass ( $M$ ) is equal to  $4(P+B)+L+S$ , and adiposity ( $A$ ) is  $L/M$ .

### 2.1. Maximising time to starvation

In the absence of any dependence of reproductive value on state at the end of the interruption (i.e. the animal either survives or dies) the optimal strategy can be found analytically (Appendix A). In this case the optimal strategy (denoted by  $\delta^*$ ) consists of first acquiring all energy from protein (if the amount of protein is more than is required to maintain the animal until the fat is exhausted) and then switching to using only lipid for energy. Thus the protein use strategy has two distinct phases, with no period in which energy needs are met from protein and fat simultaneously. There are always protein requirements so the optimal strategy is to use protein until it is diminished to the point that the protein requirements of tissues will cause it be exhausted at the same time that fat reserves are exhausted (Fig. 1a). Surplus protein is catabolised first

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