



Review

The multifaceted effects of starvation on arthropod behaviour



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Starvation is defined as a failure to consume food following an extrinsic limitation. By focusing on arthropods, I provide here a detailed review of how starvation affects foraging behaviour, predation avoidance, aggressive interactions and reproductive behaviour. Behaviour following starvation is shaped by the trade-off between the value of food, which increases with hunger level, and other vital needs, such as reproduction and avoiding ending up as prey. Foraging should take place as long as its marginal benefit outweighs the associated costs, including the avoidance of other important activities. Because starvation affects both the benefit and cost of foraging, it has various effects on behaviour. Most of the behaviours of hungry animals are selected to increase the likelihood of detecting food and better exploit it. The effect of starvation on foraging has usually revealed an increase in activity, albeit also occasionally a decrease, possibly due to a lowered metabolic rate or exhaustion. Predation avoidance becomes compromised when arthropods are hungry. Such hunger is also expressed in choosing riskier but prey-richer habitats and in not avoiding dangerous behaviours. Starvation elevates aggression and competition, as well as cannibalism. However, starved individuals are not necessarily more often victorious in such conflicts. Reproductive activities, such as male courting, female responsiveness and mating duration, decrease under starvation. An exception to this are females that gain material benefits, such as nuptial gifts, and which often increase their sexual activity in the face of starvation. I suggest that several behavioural responses to starvation follow a hump-shaped pattern, such as an increase followed by a decrease in foraging and aggression intensities with increasing hunger level. I highlight several research approaches, such as uncovering the link between starvation-induced changes in behaviour and fitness, and their underlying physiological mechanisms.

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Most animals experience spatiotemporal fluctuations in food supply, varying between years, seasons and habitat quality (Dempster & Pollard, 1981; Wolda, 1978). Even within the same season there are day-to-day changes (Ben-Natan, Abramsky, Kotler, & Brown, 2004), with food clusters becoming depleted by foraging animals, leading to diminishing foraging efficiency (e.g. Mukherjee, Zelcer, & Kotler, 2009). In order not to starve, animals experiencing a decline in food availability must necessarily respond. Responses can be either physiological, such as reducing metabolic rate to conserve energy and accumulating reserves prior to starvation (Rion & Kawecki, 2007), or behavioural, such as dispersal to other habitats where food is currently more available (Matthysen, 2012).

Starvation can be defined as a failure, usually for some extrinsic limitation, to consume food. It can be short or long (e.g. daily versus seasonal), depending on the type of limitation on obtaining food

(McCue, 2010, 2012). Other definitions also exist, such as a state in which an animal, after exploiting some of its energy storage, would feed if provided with access to food (Wang, Hung, & Randall, 2006). Fasting, in contrast, occurs when an animal skips an opportunity to eat, for some intrinsic reason, even when food is available. Such avoidance is common when animals invest in other activities, such as those related to reproduction or migration (McCue, 2010). Another difference between starvation and fasting is that a fasting animal maintains metabolic homeostasis, in order not to impede the performance of critical organs, while during starvation this is often not the case (Castellini & Rea, 1992). Most studies distinguish between three starvation phases, based on the rate of mass loss and nitrogen exploitation or on the body reserve (e.g. fat or proteins) that is being used (McCue, 2010). In mammals, the first phase refers to the period of fasting following absorption of the last meal, during which blood sugar, liver glycogen storage and some fatty acids become depleted. In the second phase, body fat reserves of adipose tissue are depleted and also some proteins. When fat is depleted the third phase begins, in which muscles degrade (Wang et al., 2006).

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Starvation-induced behaviour could be either adaptive (contributing to survival) or nonadaptive (a by-product of starvation), and it is difficult to distinguish between the two. For example, starved arthropods often invest less time and effort in reproduction (Engqvist & Sauer, 2003; Travers & Sih, 1991), which is either an adaptive behaviour, intended to conserve energy, or a nonadaptive behaviour, limiting reproductive fitness. This is a manifestation of the life history trade-off between survival and reproduction. Starvation is not categorically harmful or has negative consequences, and mild starvation sometimes contributes to performance, such as thermal tolerance or learning (Andersen, Findsen, & Overgaard, 2013; Le Bourg, 2013). Harsher starvation, however, has negative effects, perhaps similar to the differentiation between chronic and acute stress: while acute stress enhances performance, chronic stress impairs it (e.g. activity and learning: Katz, Roth, & Carroll, 1981; Prince & Anisman, 1984; Sandi & Pinelo-Nava, 2007). The result is often a hump-shaped response to stress in general, and starvation in particular.

The early models of optimal foraging did not take into account the forager's hunger level (e.g. Charnov, 1976). Later on, the physiological state was incorporated, other activities were allowed and the emphasis was no longer exclusively on the rate of energy gain but on other fitness aspects (e.g. mortality risk from predators versus starvation; Newman, 1991). These models were based on a trade-off between foraging efficiency and other important behaviours for fitness, such as predation avoidance, territory maintenance and reproduction-related behaviours, and they were either static or dynamic (Ydenberg & Houston, 1986; Mangel & Clark, 1986; Brown, 1988, 1992; Abrahams, 1993).

Foraging should take place as long as the marginal benefit of foraging is greater than the marginal cost (Brown, 1988; Mitchell, Abramsky, Kotler, Pinshow, & Brown, 1990). Starvation decreases the 'marginal rates of substitution' of energy-obtaining activities for other important activities vital for fitness, such as reproduction and avoiding predators. This lowers the marginal costs of foraging and should lead foragers to accept higher predation risk while foraging, increasing the marginal value of energy, and decreasing the marginal cost (Brown, 1988). This should lead to elevated foraging effort and avoidance of other important activities. With starvation, however, some animals reduce their metabolic rate, leading to a lower energetic cost, and in order to maintain the low metabolic rate, foraging should be delayed. Harsh starvation may lead to reduced foraging effort due to the rising energetic costs of searching. Moreover, if the expected intake rate is less than the associated costs of foraging, then a forager at any state is not expected to forage, but wait for conditions to improve while minimizing its energetic expenses. Regarding prey selectivity, models predict it should decrease in poorer habitats, when animals are hungrier, than in richer habitats (Holt & Kotler, 1987). The trade-off between foraging and reproduction, especially under starvation, could also be viewed from a life history perspective. Animals trade off survival versus reproduction, and intense reproduction leads to higher sensitivity to starvation (Scharf, Peter, & Martin, 2013; Stearns, 1992, ch. 4).

Starvation-induced behavioural responses, such as dispersal from poor-quality habitat, are often meant to enable regained access to food (Dingle, 1968; Liang, Lei, Wen, & Zhu, 2010; Oku, Vermeer, Verbaarschot, & De Jong, 2010). Whereas this behavioural response involves increasing energy expenditure, a risky move while starving, alternative behavioural responses may help to reduce the exploitation rate of body reserves, thus enabling the animal to tolerate starvation longer. One example is that of starving ectotherms seeking cooler habitats (Lazzari, 1991; Porter & Tschinkel, 1993). Two such behavioural reactions, either increasing or decreasing activity during starvation, can sometimes

be detected in the same population, constituting part of a larger behavioural syndrome (Gutman, Yosha, Choshniak, & Kronfeld-Schor, 2007). These behavioural responses depend on the marginal benefits and costs of foraging, affected by the starvation level or energetic state of the forager and by the likelihood of detecting food. In other words, a common response to starvation is first to increase activity in order to locate food, but if no food is detected, to reduce activity for the sake of saving energy, leading once more to a hump-shaped pattern of activity with starvation. It is also useful to differentiate between a temporal shortage of food, resulting from an unfavourable season, and a spatial shortage of food, stemming from poor location. The response to these shortages should be decreasing and increasing activity, respectively.

Body size has major effects on starvation tolerance, because smaller species or individuals have both less body reserves and higher metabolic rate. This could lead to earlier expression of the behavioural consequences of starvation. Moreover, larger size should increase the energetic costs of foraging and also decrease the benefit, as similar-sized prey are worth less for a large predator. Hence, larger individuals should endure starvation longer before increasing foraging activity. In both vertebrates and invertebrates, fat reserves mostly dictate starvation tolerance (Ballard, Melvin, & Simpson, 2008; Stockhoff, 1991; Wang et al., 2006). The physiology of starving animals and its life history consequences are known and have been well reviewed (e.g. Martin, 1987; Wang et al., 2006; McCue, 2010, 2012). There are surprisingly no reviews summarizing starvation-induced behaviours for any large taxa, neither vertebrates nor invertebrates. Some reviews summarize a limited impact of starvation on specific behaviours, such as sexual cannibalism (Wilder, Rypstra, & Elgar, 2009), but focus on the causes of this specific behaviour rather than on the various behavioural outcomes of starvation.

My goal here is to review the literature for such behaviours and point to the gaps in our knowledge. Specifically, motivated by the lack of reviews on the behavioural consequences of starvation, I summarize the known effects of starvation on behaviour, link them to the conceptual framework of optimal foraging and suggest understudied future directions. Before doing so, the first question should emphasize relevant or focal behaviours. Fitness depends upon survival and reproduction. Therefore, the important behaviours in which animals engage, at least from the perspective of behavioural ecology, should serve either of these two purposes, which are often traded off against one another (Davies, Krebs, & West, 2012). A popular joke by lecturers in Animal Behaviour courses relates to the four 'Fs' of behaviour that are shaped by natural/sexual selection: feeding, fleeing, fighting and mating (Pribram, 1960). I find this description useful for describing how starvation should affect the most important behaviours.

The literature is rich in studies discussing the behavioural consequences of starvation, and the list of studies I surveyed (ca. 350 papers; see [Supplementary Material](#)) is by no means complete. Starvation has longitudinal effects on all important behaviours. Some behaviours have been better studied than others, but my findings support a trade-off between risk of dying of starvation and predation. Additionally, while reproduction is clearly fundamental to fitness, when survival is at risk, reproduction is traded off with foraging. Trade-offs by starving animals that increase survival are therefore the basis of this review. I focus on arthropods as a case study, because they are large and diverse taxa, including the majority of the earth's animal species and biomass, occur in high numbers, present diverse behavioural and natural history strategies and are a fundamental component of most food chains. It is therefore easy to reach generalizations, which include the more special case of vertebrates, but I occasionally point out when generalizations cannot be reached. I therefore hope this review should

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