Exaptation and emergence as mechanisms to cross fitness valleys during evolution: an example using simulated homing behaviour

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Abstract

Evolution is often considered a gradual hill climbing process, slowly increasing the fitness of organisms. I investigate the evolution of homing behaviour in simulated intertidal limpets. In order to evolve path integration as a homing mechanism, a temporary reduction in an organism's fitness is required – since high developmental costs occur before a successful homing strategy evolves. Simple hill-climbing algorithms, therefore, only rarely result in the evolution of a functional homing behaviour. The inclusion of a second behaviour (trail-following) greatly increases the frequency of success of evolution of a path integration strategy. Initially an emergent homing behaviour is formed combining path integration with trail following. This also demonstrates evolution through exaptation, since the original role of trail following is likely to be unrelated to homing. Analysis of the fitness landscapes of homing in the presence of trail-following behaviour shows a high variability of fitness, which results in the formation of 'stepping-stones' of high fitness across fitness valleys. By using these stepping-stones, simple hill-climbing algorithms can reach the global maximum fitness value.

Introduction

In both real (biological) evolution and artificial evolution (evolutionary algorithms), a key concept is the gradual climbing of a 'hill', which represents fitness of the organism (Gould and Lewontin, 1979; Holland, 1992). Small changes to the genotype, arising through mutation or a specific recombination of genes, result in some individuals being better adapted to their task than in the previous generation. These individuals will be more likely to reproduce or produce more offspring than individuals with no advantage, or with disadvantages over previous generations (reviewed by Gould, 2002). An accumulation of these small changes will result in genes that have evolved to be well adapted to their environment (Dawkins, 1996).

Researchers who optimise problems using genetic algorithms understand that the hill climbing process is only part of the solution to finding optimal solutions (Holland, 1992). Hill climbing is likely to find a local optimal value, and to find the true, global optimal solution requires the crossing of a local minimum point, or fitness valley, on the fitness landscape (Wright, 1931). Genetic algorithms, therefore, use a range of small hill-climbing mutations, along with larger mutations, immigration and complex recombination to locate these global optimum points (Mitchell and Forrest, 1998).

It is not possible to accurately represent the true fitness landscape of a living organism, however it is logical to expect that local optimum points will occur in real evolution (Wright,

1931; 1935; Fear and Price, 1998). An example is one theory of the evolution of insect wings, which may only provide a selective advantage when large enough for flight and a possible selective disadvantage when not large enough (Brodsky, 1994). Large mutations are normally fatal or disadvantageous in animals (Gould, 1992; Watson, 2002) so it is unclear how these fitness valleys can be crossed. One explanation is that they are not crossed, but the inclusion of extra dimensions effectively allows these local optimum points to be by-passed (Cariani, 2002). Essentially these extra dimensions can be thought of as extra components of an organism's ecological niche. Another explanation involves plasticity of the phenotype of an organism, combined with genetic change – commonly known as the Baldwin effect (Mills and Watson, 2006).

In this paper, I use a simple example of a invertebrate behaviour (limpet homing) to demonstrate that emergent behaviours, arising from a combination of two or more existing behaviours, one of which had evolved for a different purpose (exaptation), can play an important role in crossing these fitness valleys; supporting the theory originally proposed by Gould and Vbra (1982). Once these emergent behaviours have arisen and the valley has been crossed, simple hill climbing evolution can operate again.

Homing in intertidal limpets

Many animals need to return to a home site after foraging. Several groups of cognitively simple animals have been studied, including limpets (Cook, 1969; 1971; Cook et al., 1969; Chelazzi et al., 1998) and ants (Muller and Wehner, 1988; Collett et al., 2003a). For each group, a suite of strategies has been proposed as potential mechanisms for homing. The most widely proposed mechanism is a system of path integration or dead reckoning, where the animal is able to approximate a vector of return by integrating the distances and angles of the outward route (Cook, 1969; Müller and Wehner, 1988; Andel and Wehner, 2004).

A further mechanism proposed for successful homing is the following of outgoing trails. Species of ant are known to deposit pheromone trails (Hölldobler and Wilson, 1990) and limpets achieve locomotion through the laying of mucus trails on the shore (Davies and Hawkins, 1998). Limpets do not generally follow trails in their entirety, from when they finish foraging back to their home, as such a mechanism would greatly increase the distance moved by the animal. They may, however, integrate a trail following mechanism with a path integration mechanism. Indeed manipulative experiments suggest more than one mechanism is used in homing (Cook,

1969; 1971; Cook et al, 1969). If the path integration mechanism is not totally accurate then the animal may not directly locate its home but may locate its outgoing trail from the home or a trail from a previous excursion and follow it back to its home. Some species of intertidal snails even show a tortuous movement phase at the start of their foraging activity that may maximise the chance that a trail is located on their return trip (Stafford and Davies, 2005). Developing two strategies to achieve a simple behaviour may appear costly, but both simple precursors of path integration (a basic sense of direction based on hydrotaxis which may help avoid predation by maintaining the animal's position in the area wet by the incoming tide rather than being fully submerged e.g. Davies et al., 2006; Ng and Williams, 2006) and trail following (used in other behaviours such as maximisation of food intake Edwards and Davies, 2002) already exist in many species of intertidal snail. These behaviours are unlikely to be evolved sufficiently to act as a homing mechanism since their presence has not resulted in the evolution of homing behaviour in many other species of intertidal snail (e.g. Stafford et al., 2007).

Complex information processing systems, such as accurate path integration, are developmentally costly to produce. This cost often results in sub-optimal behaviours occurring since the cost of development of the neural systems may outweigh the fitness benefits of the optimisation of the trait (Parker and Maynard-Smith, 1990, see also examples of deviation from optimal values of sex allocation in parasitoid wasps due to information processing or neural constraints – e.g. Hamilton, 1967; Herre, 1987; West and Sheldon, 2002). In this study, I present a developmental cost function combined with a measure of homing success and efficiency to evaluate the fitness of a given homing strategy. The strategy is modelled by a series of numerical parameters that define the probability of different decisions and the level of development of different mechanisms of homing. For example, the accuracy of the path integration mechanism is defined by developmental costs, where, as accuracy increases to 100 %, the cost increases exponentially. The homing success is measured by the ability to locate the home position and by the time taken (or distance moved) to locate the home.

Methods

Homing algorithm

The modelled limpet starts moving from the centre (position 150, 150) of an arena 300 x 300 units in size. The animal moves for 100 timesteps to simulate a foraging expedition (Figure 1). At each timestep the animal moves from its current position to one of the eight surrounding units of the arena (including diagonal movement). The initial direction of movement is randomly generated between 0 and 360 degrees and the resultant movement simulated by randomly generating an angle from a normal distribution (mean = 0, S.D. = 20). The generated angle is added to the angle at the previous timestep to create a cumulative angle, which specifies the direction of movement. At the end of the foraging phase, the angle and distance required to arrive at a home location are calculated. An error term, the maximum size of which is determined by the evolved path integration strategy, is added or subtracted to the 'correct' path integration angle or distance:
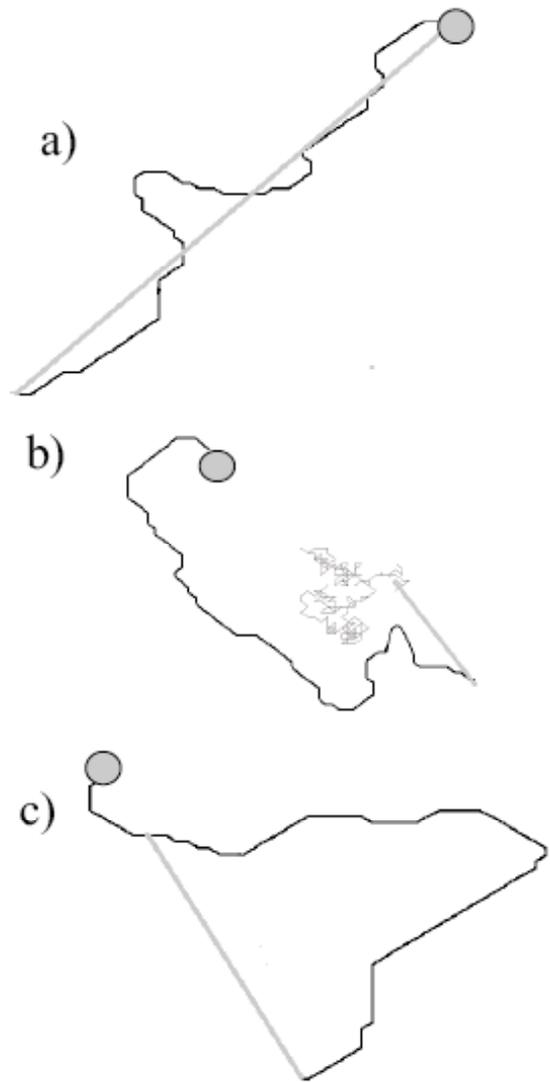

Figure 1. Example foraging paths and homing strategies used by simulated limpets. (a) indicates a successful path integration. (b) an unsuccessful path integration caused by errors in angle and distance, followed by an unsuccessful search phase. (c) a combined homing strategy, where path integration with errors results in finding a trail to follow back to the home scar. Grey circle indicates position of home scar.

$$P_{limpet} = P_{actual} + e \quad \textbf{or} \quad P_{limpet} = P_{actual} - e$$

where P_{limpet} is the path integration angle (in degrees) or distance (in grid cells) of the limpet, P_{actual} is the true path integration angle or distance and e is error induced in the limpet's path integration as a random variable between 0 and E_{max}. E_{max} is initially set at 50 for both parameters and for each individual in the population, but is altered by the hill climbing evolutionary algorithm (see below) for each individual in

successive generations. Either equation has an equal chance of occurring (i.e. the error in angle can be either clockwise or anticlockwise and distance can be either less or greater than the true distance). The Developmental cost of the process is given by:

$$C = exp^{5-(Emax/25)}$$

Costs also relate to how rapidly the limpet can find its home scar after foraging. If the limpet encounters its true home position on the way to its calculated home position then it will stop. If the home position is not located it will begin to search for a further 100 timesteps using a tortuous movement pattern, altering its bearing by an angle from a normal distribution (mean = 0, S.D. = 200) at each timestep (Figure 1b). Movement costs were 1 unit per timestep moved during path integration, 3 units per timestep whilst searching and a further cost of 400 units was imposed if the home scar was not found. The high costs of moving during the search phase and if the home scar was unable to be located were indicative of the high levels of desiccation stress and increased risk of predation that the limpet would face if moving during emersion or not finding the home scar.

The values of the relative costs are designed to create a fitness valley in the evolution of the behaviour, and are not based on empirically derived values. In this study a perfect path integration angle and direction has a cost of ~ 300 units, where as being unable to find a home scar has a cost greater than this, between 700 and 900 units, depending on the path integration distance moved and the degree of path integration precision evolved. Fitness of a given homing strategy is calculated simply as cost multiplied by –1, so fitness rises as costs reduce.

In some simulations, an ability to follow outgoing trails back to the home scar is included (Figure 1c). If a trail is encountered it may be detected by the limpet. This is decided by comparing the parameter P_{trail}, initially set at 50 units, to a uniformly randomly generated number between 0 and 100, if P_{trail} is less than the generated number then the trail is detected. Since the distance home following a trail is higher than through path integration, trails are only followed in the second half of the path integration phase or during the search phase (Stafford and Davies, 2005). The developmental cost of increasing the likelihood of trail detection is calculated in the same manner as before:

$$C = exp^{5-(Ptrail/25)}$$

Hill climbing algorithm

The hill-climbing algorithm used was not a gradient based method, but based on evolutionary algorithms that only allow for small mutations and do not demonstrate any form of recombination or crossing over; also known as evolutionary strategies. An initial population of 30 individuals were generated, all having genes coding for the two parameters of maximum angle error (*Angle*), maximum distance error (*Distance*) and, in some simulations a third parameter, the ability to detect trails

(*Trail*). All individuals initially had values of 50 for all of the genes simulated, indicating some 'sense of direction' and ability to detect mucus trails that are likely to be required for other behaviours (see above). For each generation the best six individuals were each cloned five times, to give a new population of 30 individuals. Four of each of the five clones produced from each individual were subject to small mutations in each gene between +10 and -10, where the value was determined by a random number from a uniform distribution. The algorithm was run for either 100 or 200 generations (details given in results).

Results

Using only the path integration strategy, homing behaviour (defined as > 70 % of individuals in a generation successfully locating their home position) did not frequently evolve over 100 generations of the hill-climbing algorithm (only in 4 % of cases from 100 trials). In most of the cases where homing did not evolve only between 10 and 30 % of individuals found their home position in the final generation. The inclusion of trail following resulted in a far greater success of individuals evolving a homing strategy (67 % of cases resulted in > 70 % of individuals homing). In most cases, in the absence of trail following, both *Angle* and *Distance* parameters tend to increase over time (becoming less accurate), creating a slight increase in fitness as their developmental costs decrease (Figure 2a & b).

With the inclusion of trail following, homing frequently evolved as a stable strategy (e.g. Figure 2c). Increasing the accuracy of the *Angle* parameter results in a good chance of an outgoing trail being detected during the path integration phase, and this is then followed back to the home scar (The strategy indicted in Figure 1c). This strategy can occur early in the evolution of homing, where values for the *Angle* parameter and *Trail* parameter are low (therefore the error in the angle is low and the ability to detect trails is high), but the *Distance* parameter is subject to large errors (Figure 2d; but note alternative example shown in Figure 3b, where the *Distance* parameter decreased first). This homing strategy can be considered an emergent behaviour based on the definition by Holland (1998), since it arises from a combination of two behaviours that may have developed in real animals for different purposes. Once the emergent behaviour begins to work well, fitness increases sharply and the *Distance* parameter rapidly becomes more accurate, creating an effective path integration strategy. In the example shown, the development of this behaviour means that the less efficient emergent homing behaviour, using both path integration and homing, is no longer required and begins to 'dis-evolve' to save on the fitness losses incurred due to high developmental costs (Figure 2d). This may not be true

in real limpets since trail following behaviours have a variety of roles other than in homing.

The role of trail following can be seen if the fitness landscape of the path integration function is displayed (Figure 3a). Fitness valleys can be seen as the costs of developing an accurate A*ngle* and *Distance* path integration mechanism increase. The data displayed is average data for ten replicate homing trials for each set of parameter values, nevertheless, the randomly determined nature of many of the model factors produce points where fitness is higher than for adjacent parameter values. These points represent stochastic noise, where a high proportion of the replicate homing trials generated small errors for *Angle* and D*istance* parameters by chance. Plotting the movement into the fitness valleys occurred, perhaps based on stochastic noise by the inbuilt variability in the homing model (Black plot - Figure 3a).

With the inclusion of the trail following parameter in the fitness landscape, with a value of 50 for all combinations of *Angle* and *Distance*, there was no dramatic change in the fitness landscape with fitness valleys still visible (Figure 3b). The main difference in the fitness landscape was that it was more variable with more points of high fitness where large proportions of replicate trials resulted in a high fitness. In this case, the path integration parameters were able to cross the fitness valleys and reach a global maximum fitness. The reason for this seems to be that the high variability creates 'stepping stones' of high fitness across the fitness valleys, which allow them to be crossed with only the small parameter changes allowed in the hill climbing algorithm. Since variability of the fitness landscape was lower without trail following, there was less chance of 'stepping stones' occurring in the correct positions, and a lower number of replicate trials resulted in the evolution of a homing behaviour.

Discussion

Gradual hill-climbing, as a mechanism of evolution often appears logically to be impossible in achieving complex behaviours, since a decrease in fitness is often likely to be part of the process. Although this was originally indicated by
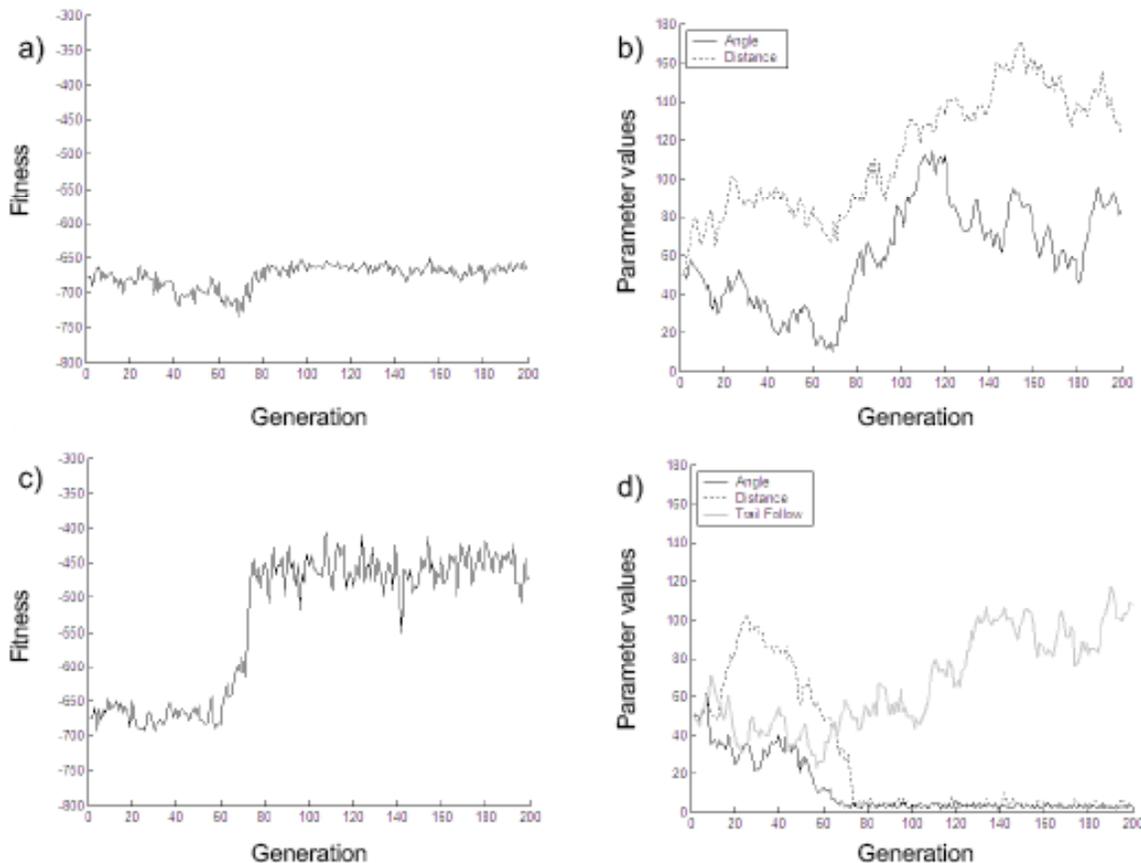

Figure 2. Fitness and the values of the homing parameters in example runs of evolution of homing behaviour. (a) Fitness in the absence of trail following, note scale is negative and theoretical maximum fitness is zero. (b) Path integration error parameters in the absence of trail following. (c) Fitness in the presence of trail following. (d) Path integration and trail detection error parameters in the presence of trail following.

Sewell Wright in his discussion of fitness landscapes (Wright, 1931; see also Fear and Price, 1998), the concept can be clearly understood by those that work on genetic algorithm optimisation processes, where the avoidance of local optimal points is the subject of much research (Holland, 1992). Clearly, the problem of artificially evolving the simple homing behaviour in this study could be solved by complex genetic algorithms with the inclusion of recombination or large mutations. These large changes in genomes are uncommon in nature, but are possible during rapid speciation events through processes such as polyploidisation (reviewed by Tate et al., 2005) or hybridisation (reviewed by Rieseberg, 1997). This study deliberately used gradual hill-climbing algorithms, only allowing small changes in parameter values, to investigate how biological evolution may be able to overcome the problem of crossing fitness valleys.
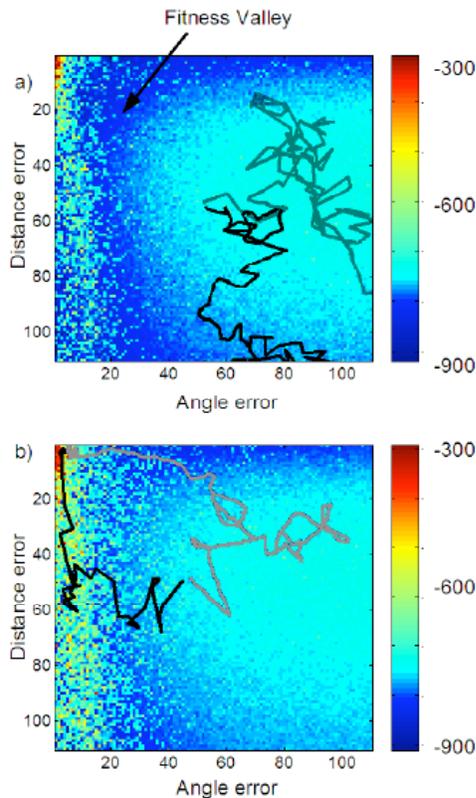

Figure 3. Evolution of the path integration parameters in fitness landscapes. Two example trials (black and grey lines) are shown both for simulations with and without trail following. Initial start positions are at coordinates (50, 50) with a perfect path integration strategy occurring at coordinates (0, 0). Landscapes were generated from estimating mean fitness for each set of parameter combinations from 10 trials of homing with these parameters. Colour bar indicates fitness (note negative values for fitness). (a) in the absence of trail following homing strategies were unable to move from light blue (high fitness) into dark blue (low fitness) areas. (b) with the inclusion of trail following (at parameter value 50) there is more variability in the fitness landscape and this created points of high fitness which allowed evolution to occur across the fitness valleys and to the point of maximum fitness.

The study demonstrates that combining several behaviours to create an emergent behaviour may provide a mechanism to cross fitness valleys, essentially since the emergent behaviour alters the fitness landscape so a drop in fitness is not required. In this study, true emergence of the homing behaviour involving path integration and homing did not occur, since both the behaviours were pre-programmed to allow homing to occur. However, both behaviours do occur with a limited degree of accuracy in numerous intertidal snails, for purposes other than homing, and provide direct selective advantages to the individuals that possess the behaviours. In a real animal, where there was no teleological goal of homing, the combination of these behaviours to create a homing behaviour, and thus increase the fitness of the animal, would be an example of an emergent behaviour (Holland, 1998).

The role of emergent properties in evolution is not a new theory. It was originally proposed by Gould and Vrba (1982) and Vrba (1983), but considered untestable, since it was not possible to identify all the lower level factors that would contribute to the emergent behaviour (see discussion in Gould, 2002). However, key to this paper is the term exaptation (also proposed by Gould and Vbra, 1982), the evolution of one structure or behaviour for a particular role, which is eventually utilised for a different role. Here, trail following could be selected for with immediate benefit to increase the intake of food, not as a functional homing mechanism. The development of the theories of emergence and self-organisation has increased rapidly since Gould and Vbra's paper (reviewed by Resnick, 1997; Camazine et al., 2001) and the application of simple computer simulations, such as presented in this paper, now allow for tests of these theories in evolutionary biology.

In the real world, many homing animals appear to rely on two or more integrated strategies to successfully home (Cook, 1969; Collett et al., 2003a). For example, when foraging, limpets are known to follow trails, yet do not follow these in their entirety (Chelazzi et al., 1998), effectively using the intermediate strategy evolved in this model. Ants such as the desert ant are known to use image matching of visual landmarks to correct the path integration mechanism and successfully home (Collett et al., 2003a; 2003b; Collett and Graham, 2004). This integration of strategies may indicate the costly nature of development of complex neural pathways for path integration. Fiddler crabs, however, do appear to rely heavily on path integration to locate refuges (Cannicci et al., 1999). Here, a high directional sense has evolved. This may be because fiddler crabs home in response to potential predators, or incoming waves – where the fitness of the animal may be far more dependent on rapid and accurate homing than in animals returning to a home position to alleviate desiccation stress over an entire tidal cycle.

This study has shown that combining two or more behaviours can result in emergent behaviours that are capable of crossing fitness valleys. Essentially this has occurred through the inclusion of extra dimensions to the modelled ecological niche of the animal (by including trail following), thus supporting the ideas of bypassing local optimal points as proposed by Michael Conrad (reviewed in Cariani, 2002). The results complement theories into how fitness valleys can be

crossed by changing the fitness landscape, particularly through phenotypic plasticity (Whitlock, 1995, Price et al., 2003; Price, 2002; Mills and Watson, 2006). Changing fitness landscapes through processes such as phenotypic plasticity or emergence may provide many insights into how evolution occurs. For example, emergence can occur at many hierarchical levels of biological organisation and may help explain how some processes, which logically appear to be unable to evolve, can in fact do so. The theory may even help discredit the 'intelligent design' theories that have been proposed to explain the inability of evolution to create certain complex molecular structures (Behe and Snoke, 2004).

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