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Energetics, cost reduction and functional consequences of fish morphology

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Cost reduction strategies are often invoked as explanations when studies of adaptation fail to find predicted costs. This might seem discouraging, offering little opportunity for further investigation. In this paper, we demonstrate that cost reduction strategies can themselves be investigated by arguments from design. Recent work on inducible morphological defences has shown that hydrodynamical disadvantages (e.g. high drag) in fishes can be compensated for by standard metabolic rate (SMR) adjustments. Here, we theoretically investigate the possibilities and limitations for swimming cost compensation through SMR adjustment. We continue by modelling how intraspecific power curve variation affects the optimal swimming velocity between food patches. Our results show that, even though SMR modifications may compensate for hydrodynamical disadvantages, low-drag fishes will nevertheless have a marked advantage under high food abundance. The relative advantage will decrease with decreasing food levels. We also show that hydrodynamical properties of fishes can be used to predict their propensity to become foraging (or swimming) specialists. Low-drag fishes can use a broad range of swimming velocities without substantial increases in swimming cost, whereas the cost of deviating from the optimal swimming velocity increases markedly in high-drag fishes. The results have important implications for the evolution of morphological diversity in fishes.

Keywords: cost reduction; swimming; foraging; standard metabolic rate; fish morphology

1. INTRODUCTION

The link between morphology, physiology and ecological performance is central to the study of adaptation and has emerged as a main focus of modern evolutionary ecology (Lauder 1996). Functional analysis combined with optimality modelling has successfully explored this connection by relating design features to measures of performance, often with great predictive power (e.g. Pennycuick 1989; Webb 1993; Losos *et al.* 1997). However, one aspect has remained elusive. Phenotypes which deviate from performance optima are commonly predicted to suffer increased costs (e.g. Dodson 1984), but such costs have often proven negligible or absent (Spitze 1992; Tollrian 1995). This has led to the suggestion that disadvantages can be avoided through cost reduction strategies (Tollrian 1995; Møller 1996; DeWitt *et al.* 1998). However, if costs can disappear this could be a serious problem for the study of adaptation in general. In this paper, we demonstrate that cost reduction strategies can themselves be investigated by arguments from design. Our approach identifies the possibilities and limitations of such strategies and leads to specific predictions about their ecological and evolutionary consequences.

The study of animal adaptation often involves the analysis of energy budgets (e.g. Pennycuick 1989; Webb 1993). Whenever it does, the metabolic rate at rest plays an essential role. In mammals and birds, this is usually estimated as the basal metabolic rate (BMR), while the measure used for most other organisms is the standard metabolic rate (SMR). Both measures have traditionally been seen as more or less fixed, species-specific consequences of the animal's body mass (e.g. Peters 1983). Recent work has fundamentally changed this view by demonstrating both considerable intraspecific variation and adaptive flexibility in the BMR and SMR (Ricklefs *et al.* 1996; Piersma & Lindström 1997; Secor & Diamond 1998). In fishes, downregulation of the SMR may enable increased growth (Wieser & Medgyesy 1990) and variation in the SMR can be used to explain fish growth strategies and life histories (Metcalfe *et al.* 1995; Metcalfe 1998). In the dimorphic crucian carp *Carassius carassius*, differences in the SMR correspond to differences in morphology (Pettersson & Brönmark 1999). Crucian carp increase in body depth in response to chemical cues from piscivorous fishes and the deeper body constitutes a morphological defence against gape-limited predators (reviewed in Brönmark *et al.* 1999). Brönmark & Miner (1992) suggested that the deep-bodied morphology should incur a fitness cost related to increased energy expenditure during swimming. However, deep-bodied fishes have a significantly lower SMR than shallow-bodied individuals (Pettersson & Brönmark 1999). As a result, the two morphs experience similar costs of transport despite marked differences in drag (Pettersson & Brönmark 1999). Could this be a strategy for reducing hydrodynamic disadvantages (Videler 1993)? If so, should we expect it to be widespread, also occurring in other types of polymorphisms (e.g. Smith & Skúlason 1996)? Here, we address the problem by focusing on two idealized morphs which differ with respect to body drag and, hence, the cost of swimming. We then continue by addressing the functional consequences of SMR adjustment. Finally, we derive optimal swimming velocities and growth rates for these fishes when living in a patchy environment.

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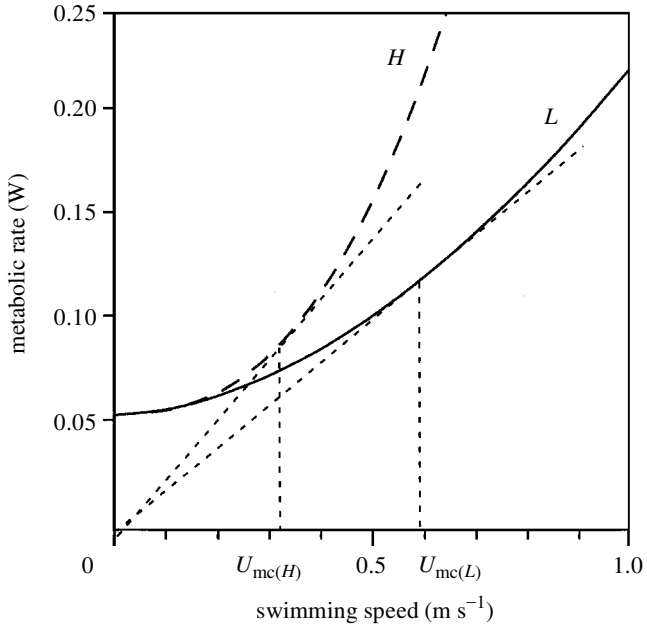

Figure 1. Graphical illustration of the metabolic cost in relation to swimming velocity in fishes. The metabolic cost for the low-drag morph is $P_L(U) = 0.0525 + 0.165 \cdot U^{1.825}$ (solid line denoted L) and for the high-drag morph is $P_H(U) = 0.0525 + 0.6 \cdot U^{2.5}$ (broken line denoted H). The swimming velocity associated with the minimum cost of transport (U_{mc}) is found by drawing a tangent from the origin to the power curve. The metabolic relationship used for the low-drag morph is for a 300 mm, 250 g sockeye salmon (*Oncorhynchus nerka*) according to Webb's (1993, p. 61) recalculation of the metabolic data found in Brett (1964). The function used for the high-drag morph is based on the same relationship, but the parameters *b* and *c* have been chosen to correspond to the relative disadvantage (steeper power curve) of the high-drag morph of the crucian carp *Carassius carassius* (Pettersson & Brönmark 1999).

2. SWIMMING ENERGETICS AND COST REDUCTION

We begin our analysis by considering the shape of the swimming cost function and its consequences for characteristic velocities. When describing the metabolic cost versus swimming velocity in fishes, researchers typically fit one of two basic equations to data on metabolic rate (e.g. Webb 1993) (figure 1 and table 1). The exponential equation has the form

$$P(U) = a \cdot e^{c \times u}, \tag{1}$$

while the polynomial function can be written as

$$P(U) = a + b \cdot U^{c}, \tag{2}$$

where *a* represents the SMR, *b* and *c* are constants obtained from the curve fitting procedure and *U* is the velocity relative to the water. Hydrodynamically, *b* and *c* represent the drag of the body, including efficiencies (cf. Webb 1993). Both equations have the dimensions work per unit of time. Two typical polynomial relationships are shown in figure 1, illustrating how power for one high-drag morph and one low-drag morph increases curvilinearly with increasing swimming velocity. For simplicity, we have assumed that these morphs differ only with respect to curve shape. Throughout this study, we will model cost reduction as a 40% reduction in the SMR, i.e. *a*, of the high-drag morph. A similar SMR reduction has been found in deep-bodied crucian carp (Pettersson & Brönmark 1999).

To derive the velocity associated with the minimum cost of transport, i.e. the energy cost per unit distance, we set $f(U) = P(U)/U$ and solve for the minimum (cf. Weihs 1973; Alexander 1974). This velocity, U_{mc}, can also be found by constructing a tangent from the origin to the power curve (figure 1) (Weihs 1973). As a result, we find that the optimal swimming velocity U_{mc} may (equation (2)) or may not (equation (1)) be affected by SMR adjustments (see table 1). Under both equations, an SMR reduction leads to a decreased cost of transport (table 1) (Tucker 1975), either through direct cost saving (equation (1)) or through a combination of direct and indirect effects as U_{mc} decreases (equation (2)). Assuming the swimming cost functions in figure 1, a 40% reduction in the SMR of the high-drag morph is sufficient to attain the same cost of transport as the low-drag morph, thus removing the effects of the hydrodynamical disadvantage.

The power curve shapes also have other implications. For instance, they provide information about the relative cost of deviating from the optimal swimming velocity U_{mc}. If we denote this relative cost of transport ΔCOT, the relationship can be described by

$$\Delta\mathrm{COT} = \frac{P(U_{mc} + \Delta U) \cdot U_{mc}}{P(U_{mc}) \cdot [U_{mc} + \Delta U]}, \tag{3}$$

where ΔU is the deviation from U_{mc}. This equation is dimensionless. The analysis shows that low-drag morphs are capable of adjusting their swimming velocities over broad intervals at the cost of only marginal increases in COT (figure 2). In contrast, high-drag individuals already suffer major costs at small deviations from U_{mc} (figure 2). Interestingly, this effect is even more marked for SMR-adjusting, high-drag fishes (figure 2).

3. MAXIMIZING GROWTH IN A PATCHY ENVIRONMENT

Foraging fishes commonly encounter patchily distributed food (e.g. Marschall *et al.* 1989). We continue our analysis by investigating how the two morphs should adjust their swimming velocities between such food concentrations in order to maximize growth (cf. Ware 1975), which is synonymous to maximizing their net rate of energy intake (Stephens & Krebs 1986). Alternatively, the surplus energy gained from foraging could be allocated to fuel reserves or energy used for reproduction. When the fish is in a food patch, we assume that the accumulated net energy gain (*E*) follows a function of diminishing return in relation to the time spent feeding in the patch (cf. Charnov 1976). When swimming between food patches the fish pay an energetic travel cost, which will be

$$C = P(U) \cdot U^{-1} D, \tag{4}$$

where $P(U)$ is the metabolic rate of swimming at velocity *U* (e.g. equation (2)) and *D* is the distance between food patches. The growth rate, measured as energy per unit of time, can be written as

$$G = (E - C) \cdot (t_p + t_t)^{-1}, \tag{5}$$

Table 1. *Two equations used to describe the relationship between metabolic cost and swimming velocity in fishes*

(The predicted optimal swimming velocity (U_{mc}) associated with the minimum cost of transport, the cost of transport (COT) and the influence of a reduction in the SMR (parameter a) on U_{mc} and COT. Parameters b and c represent the drag of the body, m is the body mass, g is the acceleration due to gravity and U is the swimming velocity relative to the water. Please note that when using the exponential metabolic function (equation (1)), only c will affect U_{mc}.)

			effect of SMR (a) reduction	
power function	U_{mc}	COT	U_{mc}	COT
$P(U) = a \cdot e^{c \cdot u}$	$\frac{1}{c}$	$\frac{P(U_{mc})}{m \cdot g \cdot U_{mc}}$	—	↓
$P(U) = a + b \cdot U^c$	$\left[\frac{a}{b(c-1)}\right]^{\frac{1}{c}}$	$\frac{P(U_{mc})}{m \cdot g \cdot U_{mc}}$	↓	↓

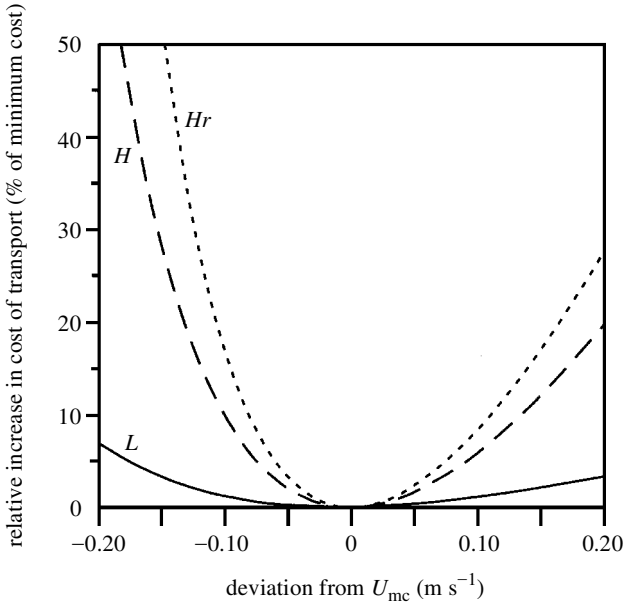

Figure 2. The cost of deviating (percentage of minimum energy required to transport unit mass over unit distance) from the swimming velocity associated with the minimum cost of transport (U_{mc} in m s^{-1}). The power equations used are low-drag morph $P_L(U) = 0.0525 + 0.165 \cdot U^{1.825}$ (solid line) and high-drag morph $P_H(U) = 0.0525 + 0.6 \cdot U^{2.5}$ (broken line). L denotes the low-drag morph, H the high-drag morph and Hr (dotted line) the high-drag morph with a 40% reduction in the SMR.

where E is the energy gain from foraging in the food patch, C is the travel cost between patches (equation (4)), t_p is the patch residence time and t_t is the travel time between food patches (cf. Thompson *et al.* 1993; Hedenström & Alerstam 1995). Now, we seek the swimming velocity which maximizes G by differentiating equation (5) and setting the derivative equal to zero. Analytically the optimal solution is given when

$$\frac{dE}{dt_p} = -\frac{dC}{dt_t} = \frac{E - C}{t_p + t_t}. \quad (6)$$

If, for simplicity, we assume a fixed net energy gain and a fixed patch residence time when foraging in a patch, then the particular solution for the optimal swimming velocity U^* between patches is

$$U^* = \frac{G + P}{P'}, \quad (\text{m s}^{-1}) \quad (7)$$

where P' is the derivative of the power function with respect to the swimming velocity (dP/dU) (Hedenström & Alerstam 1995). The general solution to equation (6) for the optimal swimming velocity and patch residence time can easily be found graphically by constructing tangents as shown in figure 3. In this case we have assumed that the low- and high-drag morphs have the same energy gain function while foraging in a food patch (figure 3). The travel cost is for a constant distance between food patches, meaning that zero travel time will be associated with an infinite velocity. However, fishes will have a minimum travel time associated with the maximum sustainable (critical) swimming speed. The two curves denoted as C_L and C_H in the left quadrant of figure 3 represent the travel costs between food patches for the two fish morphs. Additionally, C_{Hr} represents the travel cost for the high-drag morph after a 40% SMR reduction. The optimal swimming velocity is given implicitly from the travel time ($t_t = D \cdot U^{-1}$) by the mutual tangent between the gain curve and the transport cost curve (figure 3), which maximizes the overall net energy gain. Notice that the slope of this tangent also represents the overall net energy gain (equation (5)). Generally, the overall net energy gain and, therefore, the maximum growth rate is higher for the low-drag morph than for the high-drag morph. Figure 3 shows that the swimming velocity between food patches which is associated with the maximum G is higher in the low-drag morph (cheap swimming at relatively high velocities) than in the high-drag morph. The optimal swimming velocity for maximizing G is higher than the velocity of the minimum cost of transport U_{mc}, which is the velocity where the travel cost curve has its minimum (figure 3). The associated optimal patch residence time is higher for the high-drag morph than for the low-drag morph (figure 3). When the SMR is reduced (C_{Hr}), the growth rate G increases somewhat, but is still below that of the low-drag morph. The same graphical approach can also be used for analysing the effect of patch quality or foraging efficiency when in the patch (resulting in different net energy gain functions) and the effect of interpatch distances (Hedenström & Alerstam 1995). A decreased rate of foraging, e.g. as food resources decrease over the season, will yield lower optimal swimming velocities between food patches (cf. Ware 1978). The differences between morphs in net energy gain will then be lower. Furthermore, increased distances between patches will lead to reduced optimal swimming velocities between them.

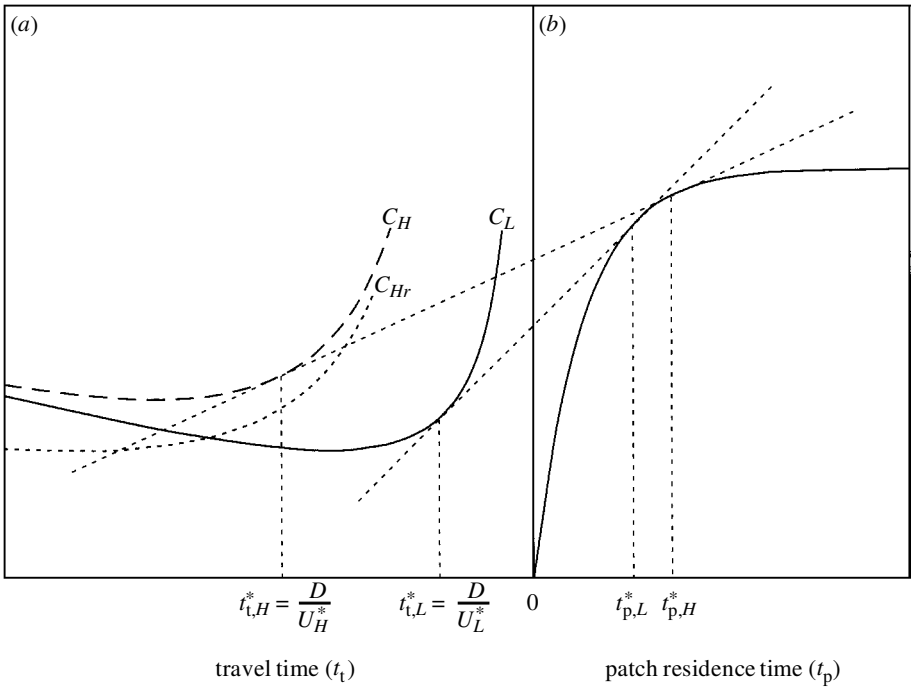

Figure 3. Graphical solution of the optimal swimming velocity between food patches when maximizing the net energy intake rate (or growth). (*a*) The transport costs between patches for two morphs of fishes. The transport time (t_t) increases from the origin towards the left and the cost curves show the minima associated with their respective U_{mc}. (*b*) An arbitrary energy gain function of diminishing return while feeding in the patch (energy gain in relation to the time in the patch, t_p). The net energy intake rate corresponds to the slope of the mutual tangent between the cost curve and the energy gain curve while foraging in the patch. The figure shows the optimal swimming velocity (calculated as D/t^*_t, where D is the distance between food patches) for fishes having high- and low-drag power equations: low-drag morph $P_L(U) = 0.0525 + 0.165 \cdot U^{1.825}$ (solid line) and high-drag morph $P_H(U) = 0.0525 + 0.6 \cdot U^{2.5}$ (broken line). C_L denotes the travel cost for the low-drag morph, C_H the same for the high-drag morph and C_{Hr} (dotted curve) the same for the high-drag morph with a 40% reduction in the SMR (optimal solution not indicated for this case). Note that the travel cost is for a fixed distance between food patches with zero travel time at infinite speed. In reality fishes experience a maximum sustainable speed (critical swimming speed) which will be associated with minimum travel time.

If a fish is foraging just to balance its energy budget without any net energy reward, i.e. $G = 0$ in equation (7), we obtain the optimum swimming velocity condition as $dP/dU = P/U$. This velocity is identical to the velocity which gives the minimum cost of transport, i.e. U_{mc}.

4. DISCUSSION

Our work shows that cost reduction strategies can be successfully evaluated by arguments from design and biomechanics. The approach not only avoids the vagueness associated with invoking general cost avoidance but also provides entirely new predictions. First, we find that high hydrodynamical drag is not necessarily associated with a high cost of transport. By adjusting the SMR, fishes can potentially compensate for otherwise costly morphologies. Depending on the specific relationship between movement and energy consumption, i.e. the power curve, cost reductions may be the direct consequences of the decreased metabolic rate or combinations of direct and indirect cost savings. The latter is true when the power curve differs from a pure exponential shape, because reductions in the SMR then also cause U_{mc}, the swimming velocity associated with the minimum transport cost, to be shifted downwards, resulting in further cost reductions.

Furthermore, the foraging model shows that it is not possible to avoid the hydrodynamic disadvantage when trying to maximize the net energy gain from food patches. When the two morphs feed on the same food and patches, high-drag fishes will be further from their U_{mc} than low-drag fishes will be and their resulting growth rate will be lower. Reductions in the SMR will not affect this outcome. The disadvantage will be particularly marked when patch quality is high. Thus, in nature, low-drag fishes will be able to use resources more efficiently at high patch quality. This also suggests that the difference between morphs in growth rate will decrease as resources are reduced. Interestingly, this pattern was found in a field study where deep- and shallow-bodied crucian carp competed for limited food resources (Pettersson & Brönmark 1997). Despite a lower SMR (Pettersson & Brönmark 1999) which could have released resources for growth (Wieser & Medgyesy 1990; but see Priede 1985; this study), deep-bodied crucian carp grew slower than shallow-bodied competitors and the difference was most pronounced during high food abundance at the beginning of the experiment (Pettersson & Brönmark 1997). It should be noted that the present model assumes that the two morphs have similar energy gain curves. A complication occurs if the two morphs specialize in different food sources or foraging tactics (cf. Schluter 1995, 1998). If low-drag fishes are more efficient foragers while in a food patch, i.e. experience a steeper gain curve than high-drag fishes, this enhances the differences in growth rate

between morphs. However, if the opposite is true, i.e. that a high-drag morph experiences a higher feeding rate than a low-drag morph, such as benthic and limnetic morphs of sympatric sticklebacks (*Gasterosteus* spp.) (Schluter 1995), differences in the growth function would reduce the effects from differential travel costs due to hydrodynamic drag. In the stickleback system the differences in growth rate among morphs may be due to secondary adaptations of the feeding apparatus, especially in the benthic form (cf. Schluter 1995). Our model might still apply to the initial state of morphological differentiation, before any other modifications of, for example, the mouth have occurred, and may explain the initial trajectory towards ecological specializations among polymorphic fishes.

We also analysed how deviations from the optimal swimming velocity affect high- and low-drag morphs. Our results established a significant but overlooked link between hydrodynamics and the evolution of trophic specialization in fishes. The cost of transport increases sharply in high-drag fishes when deviating from U_{mc}. In contrast, the cost of transport for low-drag fishes is only marginally affected over a broad range of swimming velocities. This suggests that high-drag morphs should generally show less variable swimming velocities and should consequently have a propensity to specialize in these velocities and foraging strategies which involve low-velocity variance. Low-drag fishes may use a broad range of velocities without substantial cost increases and should thus be able to remain swimming and foraging generalists. It should be noted that these predictions are merely consequences of locomotion power curves.

Taken together, these results have important implications for the species which inspired this study (i.e. crucian carp), as well as for numerous other examples of dimorphisms and polymorphisms in fishes (Smith & Skúlason 1996) and, finally, for the general use of cost reduction as an evolutionary explanation (e.g. Møller 1996). First, we find that an SMR reduction may indeed allow high-drag fishes such as deep-bodied crucian carp to attain costs of transport similar to low-drag fishes. There is now abundant evidence for intraspecific variation in the metabolic rate (Ricklefs *et al.* 1996; Piersma & Lindström 1997; Metcalfe 1998) and SMR flexibility (Wieser & Medgyesy 1990; Piersma & Lindström 1997; Secor & Diamond 1998). However, the usefulness of this strategy is restricted by the narrow range of swimming velocities which can be used. If an SMR-reducing fish deviates from its U_{mc}, the costs of transport will soon exceed those of normal fishes. In addition, the strategy most probably incurs other costs. For instance, a low-standard metabolism is normally associated with a low maximum workload, both in terms of locomotion, digestion and food conversion (Priede 1985). Nevertheless, given the large number of trophic polymorphisms in fishes (Smith & Skúlason 1996; Schluter 1998), modifications of the SMR could be a commonly occurring strategy for reducing the impact of the hydrodynamical disadvantages caused by, for example, gape-limited predation (Pettersson & Brönmark 1997, 1999) or sexual selection (Quinn & Foote 1994). Interestingly, our analysis of the relative cost of transport shows that the shapes of power curves will themselves be a factor strongly favouring ecological segregation. This aspect will definitely merit further study.

Finally, our work shows that cost-reducing strategies are not beyond the reach of functional analysis. Instead, the explicit modelling approach allows us to assess the possibilities and limitations of cost reduction. This design perspective should be taken into consideration in future studies of how morphology, physiology and ecological performance interact, as it is likely to have profound effects on how to interpret individual behaviour, trophic interactions and, ultimately, the evolution of morphological diversity.

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