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The effect of foraging parameters on the probability that a dive is successful

Alasdair I. Houston[1*], **John M. McNamara**[2], **Jon E. Heron**[3] **and Zoltán Barta**[2]

[1]*Centre for Behavioural Biology, School of Biological Sciences, University of Bristol, Bristol BS8 1UG, UK*
[2]*Centre for Behavioural Biology, Department of Mathematics, University of Bristol, Bristol BS8 1TW, UK*
[3]*Avon Longitudinal Study of Parents and Children, University of Bristol, Bristol BS8 1TQ, UK*

In this paper, we investigate the foraging decisions of an animal that dives to obtain its food. It might seem reasonable to use the probability that the diver is successful in any dive as an indicator of habitat quality. We use a dynamic model of optimal prey choice to show that this interpretation of diving success is not generally valid. In particular, we show that diving success is not directly proportional to the overall rate of gain that can be achieved in an environment. Furthermore, some environmental factors can have a non-monotonic effect on the probability of success. For example, as the travel time to the foraging area increases, the probability of success may first increase and then decrease. We point out that the same conclusions are likely to apply in the context of mate choice, i.e. the probability of getting a mate may not be an indicator of the quality of the environment in terms of reproductive success.

Keywords: diving; optimal choice; probability of success; indicator

1. INTRODUCTION

Many species of birds and mammals hunt for food beneath the surface of water and return to the surface to breathe. We refer to such animals as divers. When foraging, a diver alternates between spending time on the surface and spending time under water. We refer to the time under water as a dive. A dive is said to be successful if the diver captures a prey item. In some species, success is relatively easy to determine because the diver returns to the surface once it has captured an item. In this paper, we consider such species and explore the way in which various parameters that characterize the foraging process influence the probability that a dive is successful. We refer to this probability as the probability of success. It might be expected that divers would dive more frequently in areas with a high probability of success. A study of the Eurasian otter (*Lutra lutra*) by Kruuk *et al.* (1990) did not find such a pattern. Success was not significantly higher in areas that were used frequently than in areas that were used less frequently. Kruuk *et al.* (1990) suggested that such a pattern might result if an otter has some information about the probability of success before making a dive in a given location, and dived 'only when and where such a dive would have a predetermined probability of success. . .' (p. 71). Kruuk *et al.* (1990) then went on to make the general point that the percentage of hunts that are successful may not provide a measure of the hunter's ability or the ability of the potential prey to escape if attacked. 'It may merely measure the likelihood that a predator will initiate a hunt after observing a situation with the potential for a capture (Kruuk 1972).' (Kruuk *et al.* 1990, p. 71).

In response to Kruuk *et al.* (1990), Ostfeld (1991) reported that the probability of success in the sea otter (*Enhydra lutris*) and the marine otter (*Lutra felina*) varied with factors such as the type of prey being hunted and the area in which the otters were diving. Ostfeld concludes that probability of success is a 'complex and enigmatic issue' (p. 260), but goes on to suggest that it may be a useful measure for 'comparing foraging strategies and habitat characteristics among and within populations of carnivores' (p. 260).

An interesting general question is whether the behaviour of animals provides a reliable indication of environmental conditions (see, for example, Croxall *et al.* 1999; Boyd & Murray 2001; Barrett 2002). In this paper, we explore how a diver's probability of success depends on the environment in which it forages. Out results show that probability of success is not a reliable indicator of environmental quality.

2. MODEL OF A DIVER

Central-place foraging theory (Orians & Pearson 1979) is concerned with the optimal behaviour of foragers that deliver food to a particular location—the central place. Houston & McNamara (1985) pointed out that divers could be regarded as central-place foragers, with the surface being the central place. In this paper, we are concerned with divers that bring at most one item to the surface. In the terminology of central-place foraging, such animals are single-prey loaders.

We assume that while in the foraging area the diver may encounter two types of prey. A prey item of type i has energy content of e_i, handling time of h_i and encounter probability of p_i. The meaning of these parameters can be given by considering a dive cycle. The cycle starts when the diver descends from the surface to the foraging area. The diver reaches the foraging area at time $t=0$ and makes decisions at discrete times $t=1,2,\ldots$. At these times, the diver encounters no prey items with probability p_0 and encounters a prey item of type i with probability p_i. If the diver does not encounter an item it has the choice of returning to the surface or continuing to search. If the

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[*] Author for correspondence (a.i.houston@bristol.ac.uk).

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diver encounters a prey item of type i, it can either 'accept' it and return to the surface or it can reject it and continue to search. If it accepts the item and returns to the surface then it takes a time h_i to handle the item at the surface. This time includes both the time to prepare the item for consumption and the time to consume it. Consumption yields an amount of energy e_i. While at the surface, the diver has to spend a time S recovering from the dive. This recovery time depends on the time τ spent travelling from the surface to the foraging area and back to the surface again and the time t spent in the foraging area. Our computations are based on the following equation for recovery time:

$$S(t,\tau) = \theta \log\left\{\frac{K}{K - m_t t - m_\tau \tau}\right\}, \tag{2.1}$$

where m_t and m_τ are the rates of oxygen consumption while searching and diving, respectively, and K is the maximum amount of oxygen that can be used while submerged. Note that θ in this equation is equivalent to $1/\alpha$ of Houston & Carbone (1992). We assume that the forager can recover while handling, so that the time at the surface is the maximum of h_i and S.

If the diver rejects the item and continues to search then the dive will eventually end either because the diver accepts a subsequent item or because it returns to the surface without an item. It can be worth returning to the surface without an item if the recovery time is an accelerating function of the time spent foraging. We refer to the foraging time at which the diver returns to the surface without an item as the maximum foraging duration, $t_{\max}$. Thus, there are two sorts of dive: successful dives that result in an item being brought to the surface, and unsuccessful dives in which the diver returns to the surface without an item.

We seek a behavioural strategy for the diver that maximizes the long-term rate of energetic gain. We refer to such a strategy as an optimal strategy. For the specific parameter values that we consider, the form of the optimal strategy is as follows. The diver should always accept the type of item that yields more energy, i.e. items of the type with the higher value of e_i. For the eider duck (*Somateria mollissima*), the type with more energy might be crabs and the other type might be urchins (Beauchamp *et al.* 1992). For the sea otter (*E. lutris*), the type with more energy might be abalone and the other type might be urchins or crabs (Ostfeld 1982). Without loss of generality, we assume that $e_1 > e_2$. Whether or not it is optimal to accept type 2 items depends on the parameter values. There are three possible cases, as follows.

(i) It is never optimal to accept type 2 items, i.e. only type 1 items are accepted until the maximum foraging duration is reached.
(ii) It is optimal to accept just type 1 items until a critical foraging duration t_c is reached. After this, it is optimal to accept both types until the maximum foraging duration is reached.
(iii) It is always optimal to accept both types of item.

If handling times are long, they may determine the time that the diver spends at the surface. In this case, the better type is not the one that yields the most energy, but the one with the higher value of e/h (cf. Houston & McNamara 1985). With the parameter values that we use in this paper, h_1 has to be very large for type 1 not to be the preferred prey type.

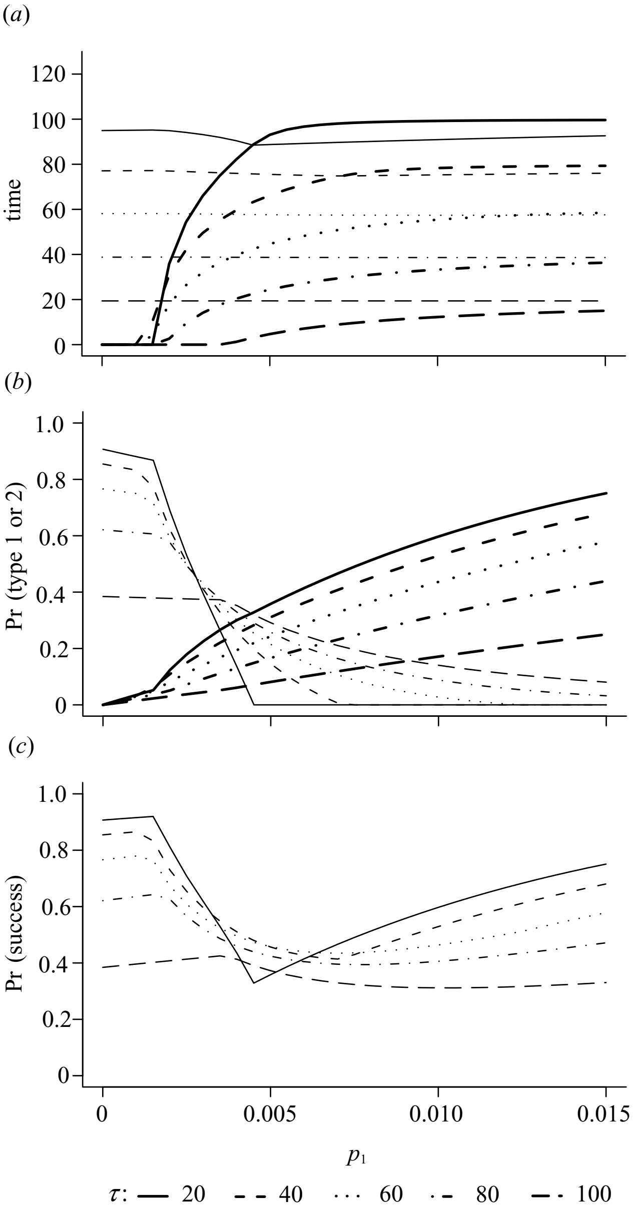

Figure 1. The effect of changing abundance of prey type 1, p_1, for a range of values of τ. (*a*) The optimal policy. The thick lines give the critical time, t_c, after which prey type 2 is also accepted; the thin lines show the maximum foraging time, $t_{\max}$, after which the animal returns to the surface. (*b*) The probability of surfacing with prey type 1 (thick lines) or prey type 2 (thin lines). (*c*) The probability of success. Parameters: $K = 120$, $e_1 = 38\,000$ (average energy content (J) of crabs; Beauchamp *et al.* 1992), $e_2 = 3100$ (average energy content (J) of urchins; Beauchamp *et al.* 1992), $p_2 = 0.025$, $\theta = 5$, $m_\tau = 1$, $m_t = 1$, $h_1 = 100$ and $h_2 = 45$.

3. RESULTS

Details of how the optimal strategy may be calculated are given in electronic Appendix A (available on the The Royal Society's Publications Web site; see also Houston & McNamara 1999). The optimal strategy specifies:

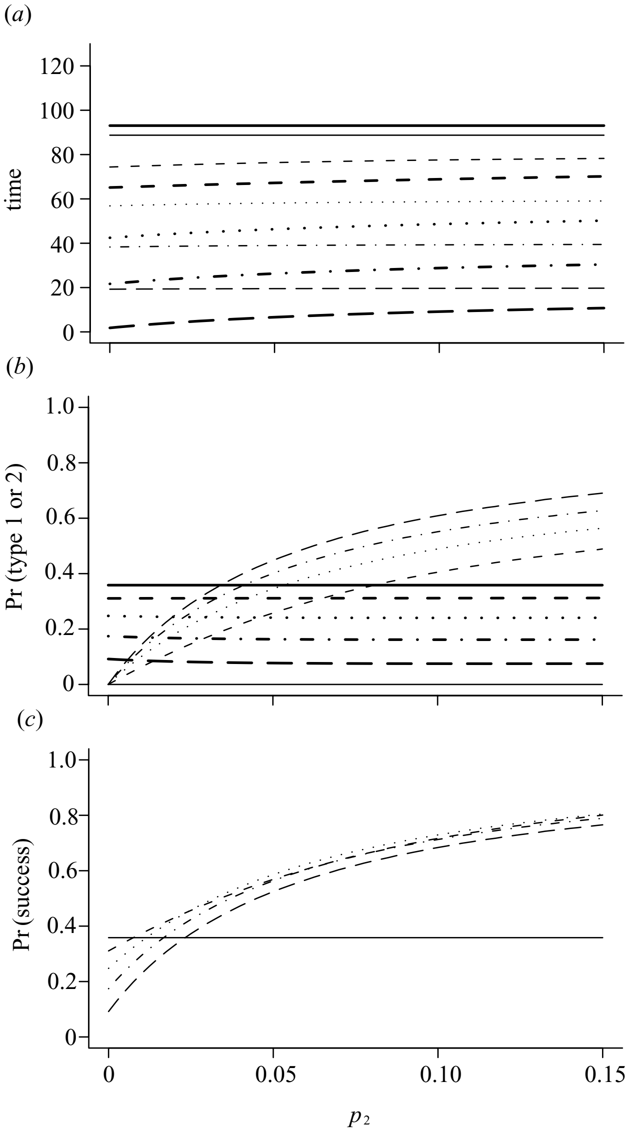

Figure 2. The effect of changing abundance of prey type 2, p_2, for a range of values of τ. For the explanation of the convention used and parameter values see the legend to figure 1.

(i) the critical time t_c at which the diver should switch from specializing in type 1 items and rejecting type 2 items to generalizing, i.e. accepting both type of items; and

(ii) the maximum foraging duration t_{max}, i.e. the time at which the diver should return to the surface without an item (see figures 1*a* and 2*a* for examples).

Given a strategy, we can compute the probability that the diver returns to the surface with an item of a given type. We can also find the probability that the dive is successful.

(a) *The effect of the abundances of the prey types*

To represent a change in the abundance of prey type *i*, we change the probability p_i that a type *i* item is encountered. Figure 1*a* shows how the optimal strategy (i.e. the critical time t_c at which it is optimal to switch from specializing to generalizing and the maximum foraging duration t_{max}) changes as p_1 is increased. When p_1 is very low, it is optimal to generalize throughout the dive ($t_c = 0$). As a result, as p_1 increases (but is still very low), the probability of surfacing with a type 1 item increases whereas the probability of surfacing with a type 2 item decreases slightly (figure 1*b*). The probability of success increases slightly (figure 1*c*). As p_1 continues to increase, it becomes optimal to specialize at the start of the dive ($t_c > 0$ in figure 1*a*). As a result, the probability of obtaining a type 1 item increases quite rapidly, but the probability of obtaining a type 2 item drops even more rapidly (figure 1*b*). The result is that the probability of success falls (figure 1*c*). As p_1 increases further, the effect on the probability of obtaining a type 1 item is stronger than that on the probability of obtaining a type 2 item (figure 1*b*) and the probability of success increases (figure 1*c*). Thus, the effect of p_1 on the probability of success is non-monotonic; the probability of success increases, then decreases and then increases again.

By contrast to the effect of p_1, the effect of p_2 is straightforward, with the probability of success increasing as p_2 increases (figure 2).

In addition to looking at the effect of abundance on success, we can also use the model to explore how abundance influences the composition of the optimal diet. Figure 3 gives some examples of the proportion of type 1 items in the diet as a function of the proportion of type 1 items in the environment. Figure 3*a* is based on varying p_2, whereas figure 3*b* is based on varying p_1. In each case, the proportion of type 1 items in the diet can deviate markedly from the proportion in the environment. Furthermore, the proportion in the diet is not determined by just the proportion in the environment. The absolute abundance and the travel time also have an effect.

(b) *Effect of travel time τ*

As τ increases, t_{max} first increases and then decreases (see Houston & McNamara 1999, fig. 4.3). This effect can be understood as follows. An increase in τ increases the time that it takes to return to the foraging area once the diver leaves. This selects for being more persistent on the current bout. However, increasing τ decreases the diver's oxygen reserves on arrival at the foraging area, and thus selects for reduced time foraging. The effect of τ results from the balance of these opposing pressures. As a consequence of the effect of τ on t_{max}, the probability of success first increases and then decreases as τ increases (figure 4).

(c) *The effect of the energetic value of prey types*

How does the energetic value of the two types of items affect the success rate? Figure 4*a* shows that increasing the energy content of type 2 items results in an increase in the probability of success for a large range of values of τ. However, in figure 4*b* we observe the opposite effect when the energetic value of type 1 item is increased.

Increasing the energetic content of type 1 items causes the diver to become more choosy (delaying the switching to the generalist strategy until later in the dive) with the result that more dives are unsuccessful owing to the scarcity of the more valuable items. This effect has nothing to do with food encounter probabilities and shows how two foraging areas could have the same prey densities but differ in their success rates.

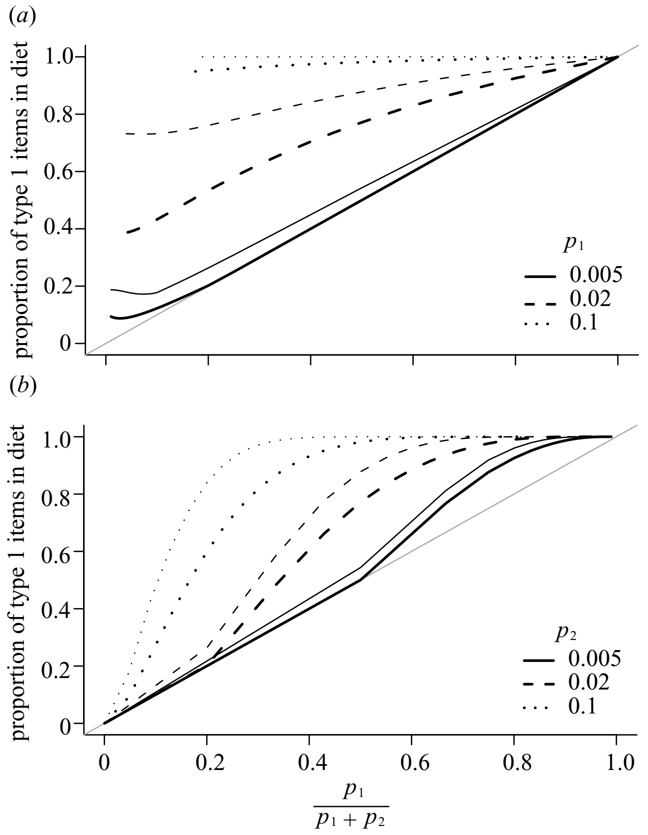

Figure 3. The effect of relative prey encounter probability $p_1/(p_1 + p_2)$ on the proportion of type 1 items in the optimal diet. (*a*) p_2 is changed while p_1 is kept constant at different values. (*b*) p_1 is changed while p_2 is kept constant at different values. Legends show the prey encounter probability that was fixed, line thickness marks different travel times (thin lines: $\tau = 30$, thick lines: $\tau = 90$). The parameters are as in figure 1 except $\theta = 50$, $h_1 = 50$ and $h_2 = 25$.

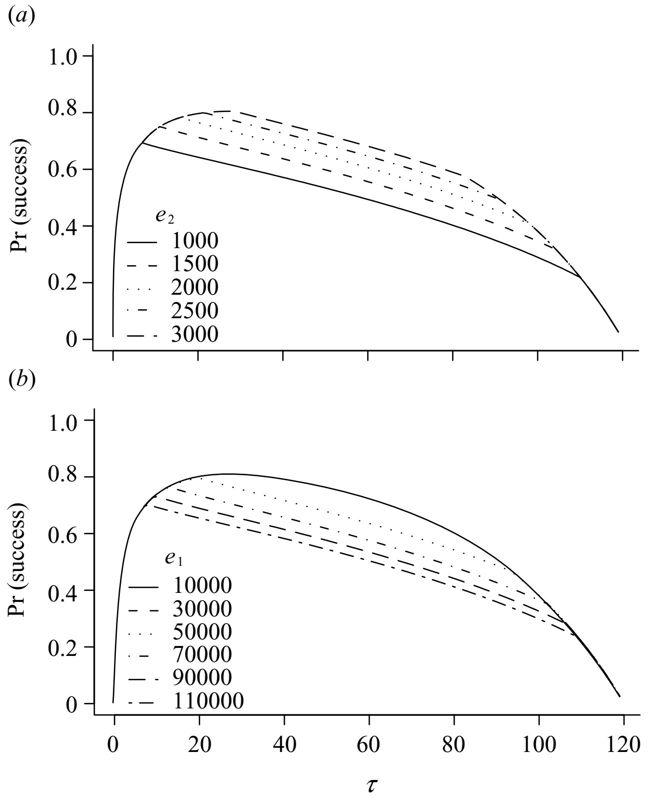

Figure 4. (*a*) The effect of changing e_2 on the relationship between success rate and travel time τ. (*b*) The effect of changing e_1 on the relationship between success rate and travel time τ. The parameters are as in figure 1.

4. DISCUSSION

The results show that the probability of success can be only of limited use as an indicator of the state of a diver's environment. In particular, our results have established the following points.

(i) The probability that a dive is successful is not just a property of conditions in the foraging area, but it also depends on the travel time τ.
(ii) The probability that a dive is successful is not always directly correlated with the maximum rate γ^* that can be achieved. For example, increasing either e_1 or e_2 both increase γ^*, but increasing e_1 decreases the probability of success whereas increasing e_2 increases the probability of success.
(iii) An environmental factor may have a non-monotonic effect on the probability of success. For example, figure 1*c* shows that as p_1 increases, the probability of success may increase, then decrease then finally increase again. Figure 4 shows that as τ increases, the probability of success first increases and then decreases.

We have illustrated these effects in particular cases, but our computations indicate that they occur over a wide range of parameter values and hence are robust. In this paper, we have assumed that the time at the surface is the minimum of the recovery time and the handling time. The same qualitative effects are found if the time at the surface is the sum of the recovery time and handling time, as assumed by Houston & McNamara (1985) and Beauchamp *et al.* (1992). The effects that we have obtained are also likely to occur in other contexts. For example, our model of selection of prey items by a diver could be modified to represent mate choice. This suggests that the probability of obtaining a mate is not likely to be a good indicator of whether a particular environment is good or bad in terms of reproductive success.

The relationship between relative abundance of prey in the environment and prey in a predator's diet can influence the stability of the prey population (Murdoch 1969; Murdoch & Oaten 1975). Ostfeld (1982) discussed the diet of sea otters in this context. Our interest is the extent to which the proportion of prey type in the diet reflects the proportion of the type in the environment. Figure 3 shows that the proportion in the diet is often quite different from the proportion in the environment. The figure also shows that the proportion in the environment does not uniquely determine the proportion in the diet.

We have shown that the probability of success is not a good indicator of habitat quality. What is required is an alternative measure that will usually be correlated with the quality of the environment. A possible measure is the switch time at which foragers will begin to accept the less-preferred food type. Such a value could be determined using the observed distribution of dive times for animals returning with either type 1 or type 2 items. A later switch time would suggest a richer environment, with the diver being more reluctant to accept an inferior prey item.

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