



Bet-hedging when Targets May Disappear: Optimal Mate-seeking or Prey-catching Trajectories and the Stability of Leks and Herds

JOHN M. C. HUTCHINSON*

School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, U.K. and School of Mathematics, University of Bristol, University Walk, Bristol BS8 1TW, U.K.

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When a female frog moves towards a calling male, the male may suddenly stop calling and the female have to switch to another male. Analogous situations where “hunters” move towards “targets” that can disappear unpredictably include predators stalking prey and plants growing towards gaps in the canopy. I use dynamic programming to show that when the hunter has a choice of such targets it is optimal to take a curved bet-hedging trajectory, initially heading between two targets so that if one target disappears the other is closer. Also hunters should prefer groups of targets, even if a solitary target is somewhat closer, because it is unlikely that all targets in a group will disappear. Assuming that hunters follow these optimal trajectories I then ask whether it will pay targets to form herds or leks. The extra attractiveness of groups in this model turns out not to be sufficient to outweigh the advantages of herding, but the net benefits of herding are considerably reduced.

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1. Introduction

The questions addressed in this paper were initially motivated by the phonotactic behaviour of female frogs and crickets towards males, several of which may often be calling close together. I consider how a female’s trajectory might be directed and shaped to hedge her bets in case the intended male disappears before he is reached; such movement rules of the females could also affect how males should space themselves. Identical principles could apply to a wider range of phenomena, including plant growth and predators hunting prey, so to

emphasise the abstract ideas I first explain the issues using a fanciful parable based on human behaviour. Having then drawn comparisons with real biological situations, I set out a simplified model and calculate optimal behaviour under its assumptions.

1.1. THE TAXI PARABLE

Imagine that there are two taxis on the far side of a wide road, parked some distance apart [Fig. 1(a)]. You need to catch one of them—it does not matter which—but other people may take one or both taxis before you have time to reach either. Taxis thus disappear unpredictably. My first question is what is your optimal trajectory. Should you head straight for the nearer of the two taxis, or should you initially

*Present address: School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, U.K.
E-mail: John.Hutchinson@bristol.ac.uk

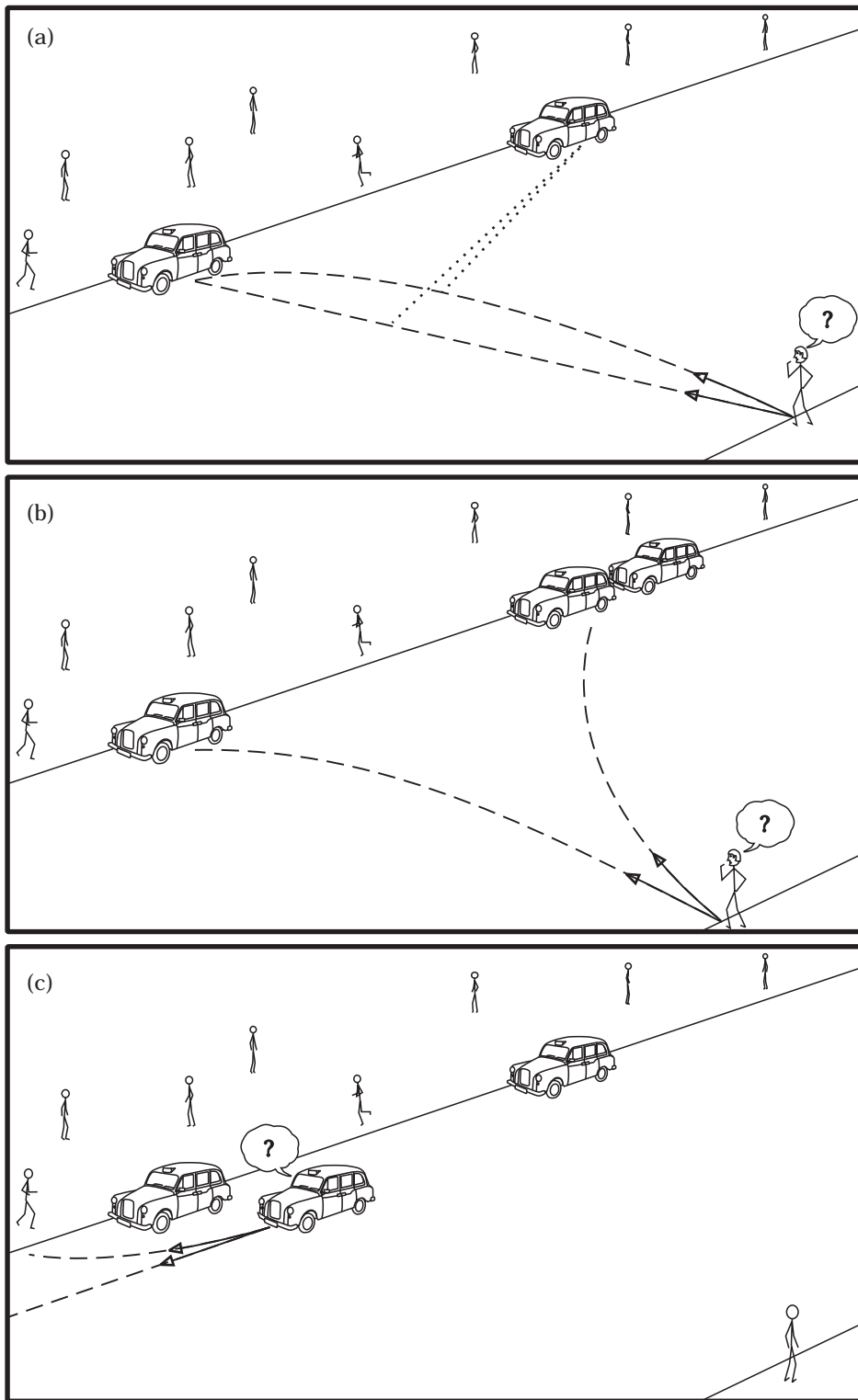


FIG. 1. The taxi parable. (a) What is the customer's optimal trajectory towards two taxis that someone else may occupy at any time? (---) are alternative trajectories (straight or curved). If the left-hand taxi disappeared the customer would head straight to the remaining taxi (..); (b) should the customer head for a pair of taxis even though a solitary taxi is nearer?; (c) assuming customers behave optimally, should a taxi park next to another?

head somewhere in-between them? The latter course means that, if the nearer taxi disappears before you reach it, you are closer to the second taxi than if you had headed straight to the nearer. This means being more likely to reach the second taxi before it too disappears. On the other hand, the curved trajectory takes longer, which makes it more likely that the nearer taxi will disappear before you reach it.

Consider now three taxis on the other side of the street, one parked on its own, the other two right next to each other [Fig. 1(b)]. My second question is which taxi should you initially head towards. There is an obvious advantage to going towards the pair of taxis, since it is relatively unlikely that both will have disappeared by the time you get there. Nevertheless it may be best to head towards the solitary taxi if it is much closer than the pair. The optimal choice of target should depend both on the positions of the targets and on your own position.

The third question considers the optimal behaviour of the taxis if they can rely on their customers taking optimal trajectories. Imagine two taxis parked some distance apart. Should a third taxi park right next to one of these, to form a pair, or should it park some distance away from both [Fig. 1(c)]? The advantage of forming a pair is that pairs should be more attractive. The disadvantage is that any customers attracted must be shared with the “partner”. So for a partnership to be stable it must attract at least twice as many customers as a solitary taxi.

The organisation of this paper is to examine and discuss each of these three questions in turn. But first I discuss some biological examples which have a structural similarity to the taxi problem.

2. Biological Applicability

The key features of the taxi scenario are that (1) the “targets” (taxis) disappear unpredictably and independently of each other, and (2) the “hunter” (customer) knows the positions of the targets and whether they are still there, but takes time approaching them. These features are shared by many species that call to attract mates, in particular frogs and crickets.

Calling frogs and crickets, which are usually the males advertising for mates, may disappear acoustically for several reasons. They may be killed by predators, they may start mating with a female, they may be disturbed in some way, or they may stop calling of their own accord, perhaps to conserve energy. In some circumstances the disappearance will not be completely unpredicted by the approaching female, perhaps because she is aware of competing females. Nor need the disappearance be totally independent between neighbours, since a caller might time any rests according to whether its neighbour is calling, and since disturbances will often affect neighbouring callers simultaneously. However, there will often be an unpredictable and independent component to when callers disappear, and it is the consequences of this for the optimal strategies that this paper is concerned to isolate.

Male frogs and crickets calling for mates are often aggregated. The model that I develop potentially might explain not only how females approach these groups of males but also why such groups form. For brevity I call these groups leks, although some authors apply this term more strictly.

Another comparable situation is of a predator approaching prey, perhaps a cat in long grass stalking birds in a flock, any member of which may fly off spontaneously at any time. In other situations prey themselves might be faced with similar choices when fleeing from a predator towards refuges such as holes in a coral reef; if another fish occupies a hole first, the refuge is suddenly no longer available. In plants and fungi one might draw comparison with roots and mycelia following nutrient concentrations to a nutrient source, or shoots seeking an opening in the canopy; either might be forestalled unpredictably, particularly by a competitor getting there first.

This paper is primarily concerned with calculating the optimal behaviour of such organisms faced with this situation of disappearing targets. Because organisms like plants may not have the sensory capabilities to achieve the optimal strategy, I will also compare the performance of several suboptimal strategies that are generated by following simpler rules of thumb.

3. Assumptions of the Model

To isolate the principles involved in hunting disappearing targets, the model makes the following assumptions:

- (1) the targets are stationary;
- (2) the hunter knows the exact position of every target;
- (3) each target disappears with the same constant probability, which is thus unaffected by the behaviour of the hunter or of the other targets. The hunter knows this probability;
- (4) a target never reappears after disappearance and no new targets appear;
- (5) the hunter knows immediately when a target disappears;
- (6) all targets have the same value to the hunter, or, equivalently, the hunter cannot distinguish the value of a target before reaching it;
- (7) there is only one hunter, or hunters do not compete or interfere with one another;
- (8) the hunter stops after reaching a target, or when there are no targets left. This and (7) imply that hunters should maximise the chances of reaching some target (rather than minimising the expected time to reach a target);
- (9) hunter and targets are situated on a flat two-dimensional landscape.

Obviously in any real situation some of these assumptions will be violated, but it is only by investigating simple models that we learn whether the principle is potentially sufficient on its own to explain aspects of real behaviour. It would be a mistake instead to start with a more complete and complex model of, say, a cheetah attacking a gazelle herd. Having started with simple models we can subsequently relax assumptions and introduce other factors one at a time, to establish which factors have important consequences and why. Section 9 discusses some relaxations of the above assumptions.

4. Optimal Trajectories: Methods

I did not find it possible to calculate the optimal trajectories analytically and so resorted to the numerical technique of dynamic programming. This technique is often used in behavioural

ecology when the trajectories are in a space of states rather than position (Houston & McNamara, 1988; Mangel & Clark, 1988). Applying the technique to find optimal movement in space proved not to be straightforward, and the Appendix explains the successful approach in detail.

5. Trajectory Shape

5.1. CURVATURE OF THE TRAJECTORIES AND THE PROBABILITY OF DISAPPEARANCE

The optimal trajectory when two disappearing targets are available is indeed a curved line initially heading between the two targets (Fig. 2). The hunters hedge their bets.

For hunters starting equidistant from the two targets, as the probability of disappearance increases the optimal trajectories become more curved (compare the dotted and solid lines in Fig. 2). Only at extremely high rates of disappearance do trajectories again become straighter, when hunters should "make a dash" for the nearer target (Fig. 3). But from more asymmetrically placed starting points the trajectories may consistently get slightly straighter as the probability of disappearance increases (Fig. 2).

Whatever the starting point, trajectory curvature is surprisingly insensitive to the probability of disappearance. Figure 3 shows how trajectory length (a measure of curvature) depends on the probability of disappearance for a hunter starting equidistant from the two targets. Mostly there is a roughly linear relationship between trajectory length and the probability of disappearance. This means that there is very little difference in the shape of the optimal trajectory when the probability of disappearance is low even when this varies by a considerable factor. The optimal trajectory does not converge to a straight line (length = 1) as the probability of disappearance approaches zero.

The explanation for this insensitivity of trajectory length is that as the disappearance probability is reduced, a curved trajectory not only less often has a benefit (the intended target rarely disappears, and if it does the alternative target will probably still stay there even if the

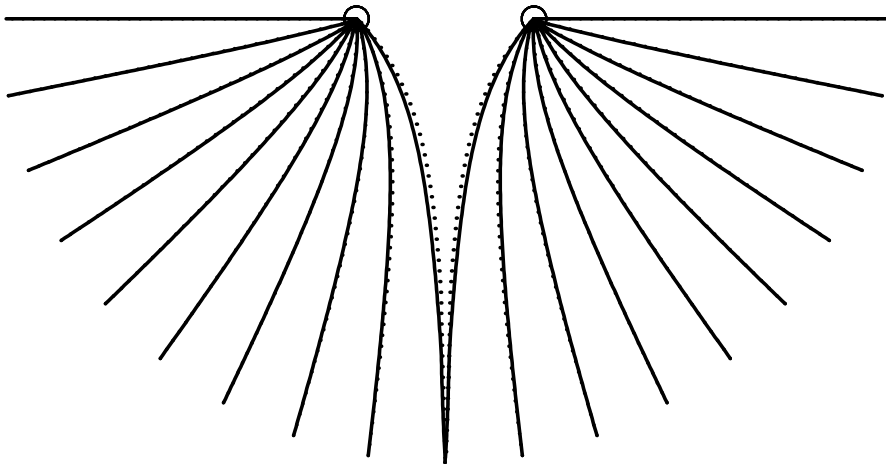


FIG. 2. Optimal trajectories from different starting positions around a semicircle towards two targets (O) that may disappear. In this and subsequent figures the trajectories shown are when no disappearances happen to occur. Trajectories from above would be a mirror image of those shown. Targets are 1 unit distance apart. For the (...) the mean rate of disappearance of each target is 0.5 per unit distance, and for the (—) it is 0.05. A trajectory for a value of 0.005 would be almost indistinguishable from the latter at this scale.

target switches direction to it from further away), but also less often has a cost. The cost is the increased chance that the nearer target disappears because the curved trajectory takes longer.

This is the only cost in the model, but in real life there will be other demands on an animal's time and/or a risk associated with being on the move. To model these extra costs I tried

incorporating a small random chance of the hunt being interrupted. Then trajectories are straighter, and as disappearance probability declines they do converge to a straight line (Fig. 3). Thus the model does not always predict that trajectories will be noticeably curved.

5.2. EVIDENCE OF CURVED TRAJECTORIES AND ALTERNATIVE EXPLANATIONS FOR THEM

Are real trajectories curved? Unfortunately I found no systematic studies of the trajectories followed by predators who already knew the location of adjacent prey items, and most mate-choice experiments on phonotactic animals place them on a line between loudspeakers or use a Y-shaped maze. However, some descriptions of Orthoptera moving towards two loudspeakers are encouraging: "the insect's path is usually an irregular arc" (Morris *et al.*, 1978), and "some continued to walk along the mid-line between the loudspeakers ... before turning" (Latimer & Sippel, 1987). Bailey *et al.* (1990) figure some trajectories; they are rather wiggly and difficult to categorise, some curved very much like my predictions but others more direct.

Unfortunately, asking merely whether real trajectories are curved is not a very critical test of my hypothesis. One reason is that, as noted earlier, the model has only to include time costs to predict much straighter trajectories.

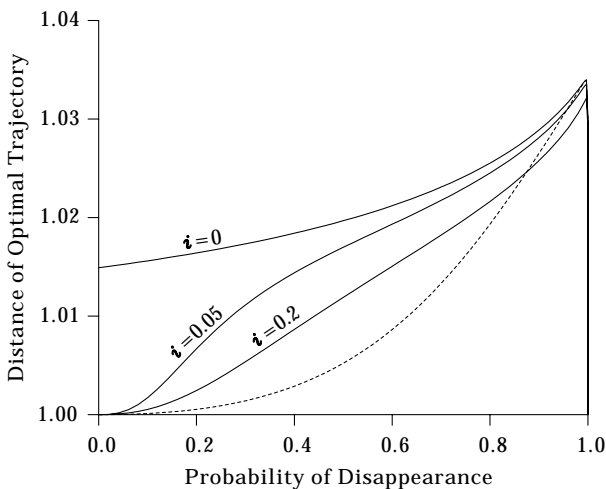


FIG. 3. The length of the optimal trajectory as a function of the probability of each target disappearing. The hunter's starting position is 1 unit of distance from two targets and the targets are also 1 unit apart. Probabilities refer to the time taken to move 1 unit. *i* is the probability that the hunt is interrupted, in which case the hunter catches neither target. (---) refers to the situation where *i* = 0 and both targets can be taken in succession; for the other lines only one target can be taken.

Conversely when curved trajectories are found, there are several alternative explanations.

One such explanation for predators' trajectories is that they initially avoid heading straight towards any particular individual in a herd because this would warn the intended target that it was at higher risk (Burger & Gochfeld, 1981, 1990). Non-straight trajectories can also be optimal when the problem is to locate targets (Benhamou, 1992). Interestingly, other explanations are closely related to the present one. The suitability or quality of a target may become apparent only on closer or longer inspection, and this source of uncertainty favours similar bet-hedging trajectories as uncertainty about disappearance (Hutchinson, unpublished). Thus by initially heading between the targets the hunter is closer to an alternative target if it recognises that the chosen target is unsuitable, and it may be able to compare target qualities better. Another source of uncertainty might be

the targets' precise locations. Thus if I allowed the targets slow random movement, or let an aerial hunter sometimes be displaced by unpredictable gusts of wind, I suspect that the hunter's trajectory should again be curved.

Other explanations for curved trajectories are based not on function but on following simple mechanisms (e.g. Fraenkel & Gunn, 1961; Helbing *et al.*, 1997; Kennedy, 1983). I now consider in particular two such mechanisms which generate trajectories that superficially resemble the optimal bet-hedging trajectories, and which might thus make good rules of thumb to approximate the optimal strategy. The next section compares how well they perform. The first simple mechanism is for a phonotactic animal to step in the direction that most increases the perceived volume of sound, i.e. to follow the steepest intensity gradient. If the signal from different targets is perceived as a summed signal, this strategy produces the curved

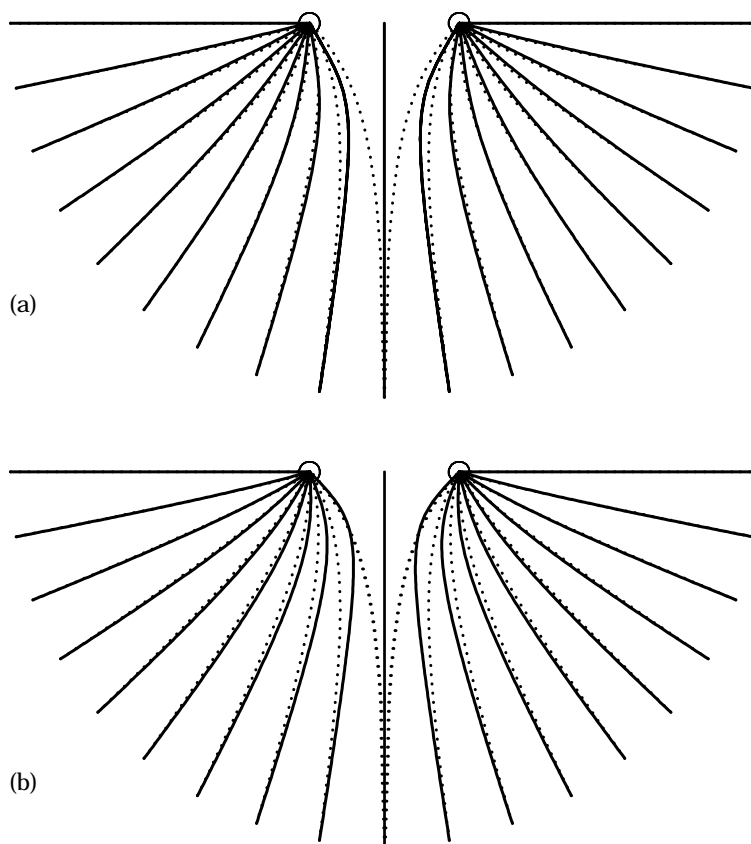


FIG 4. Suboptimal trajectories towards two targets (○). (—) in (a) are for an animal taking the steepest gradient of signal concentration, and in (b) for an animal using a triangle-of-forces rule (in both cases assuming that signals from the two targets combine additively, and decay according to the inverse square law). (· · ·) is the same optimal trajectory as is shown dotted in Fig. 3.

TABLE 1
The length and success/failure probabilities of optimal and suboptimal trajectories

Policy	Trajectory length if no disappearance	Probability reach Target 1	Probability reach Target 2	Probability no target reached
Optimal	1.018	0.601	0.208	0.191
Straight to nearest	1.000	0.606	0.201	0.193
Steepest gradient	1.309	0.539	0.253	0.207
Triangle-of-forces	1.342	0.533	0.257	0.210

Target 1 is at $(-0.5, 0)$, Target 2 at $(0.5, 0)$, and the starting position of the hunter is $(-0.0001, \sqrt{3}/2)$. The mean rate of disappearance for each target is 0.5 per time taken to move 1 unit.

trajectories in Fig. 4(a). A slightly different trajectory results if the animal moves as if attracted towards each target with a force scaling as the inverse square of distance [Fig. 4(b)]. I refer to it as the “triangle-of-forces” policy. Fraenkel & Gunn (1961) discuss the simple mechanisms by which animals can achieve such trajectories. These two sets of trajectories differ most from the optimal trajectories when the starting position is nearly symmetrically placed relative to the two targets (Fig. 4). Then the suboptimal trajectories lie nearer the line of symmetry and are longer (Table 1).

5.3. PERFORMANCE OF SUBOPTIMAL TRAJECTORIES TOWARDS TWO TARGETS

One consideration bearing on whether we expect to observe the optimal policy is the cost of not following it. In this section I compare the performance of the optimal trajectories with the performances of three sets of suboptimal trajectories: going straight to the nearest target and the two sets of suboptimal curved trajectories just discussed (Fig. 4).

The cost of a suboptimal trajectory depends on the starting position of the hunter. For instance, if the hunter is collinear with both targets the trajectories and fitnesses of all policies discussed are the same. In contrast, Table 1 shows the proportion of times that neither target is reached when starting just slightly nearer Target 1 than Target 2 and at a distance from the targets the same as the distance between the targets. For this starting position and the specified rate of disappearance the straight-line policy fails 1.4% more often than the optimal strategy, whereas the other curved policies fail 9 and 10% more often. The benefit in following the optimal policy, whilst not huge, is thus not

trivial, and might plausibly be sufficient for selection to dominate over drift. With other starting positions the failure rates of the suboptimal strategies can be in reverse order to those in Table 1. The next section examines the performance of optimal and suboptimal policies when there are three targets.

6. Choice of Target when there are Three or more Targets

So far I have considered only two equal targets, so that which the hunter heads towards depends simply on which is closer. With three targets, however, there can be an advantage in heading towards two targets that are close to each other even if the more isolated target lies closer to the hunter. The reason is that it is relatively unlikely that both of two targets will disappear. Figure 5 shows optimal trajectories when two targets are coincident and a third on its own. Hunters starting from point A should move towards the pair of targets even though the solitary target is closer. One can map out two complementary “zones of attraction” describing the hunter’s destination if no target happens to disappear; the dashed line in Fig. 5 indicates the boundary between these zones.

Surprisingly, the position of this boundary is extremely insensitive to the probability that the targets disappear (as long as this probability is the same for all targets). However, this is somewhat an artefact of the model assuming no other advantages in getting to a target quickly. If there is a small chance that the hunt is interrupted, when no targets can then be caught, the boundary of the zone of attraction is more symmetrically placed, and now becomes more so as the disappearance probability decreases.

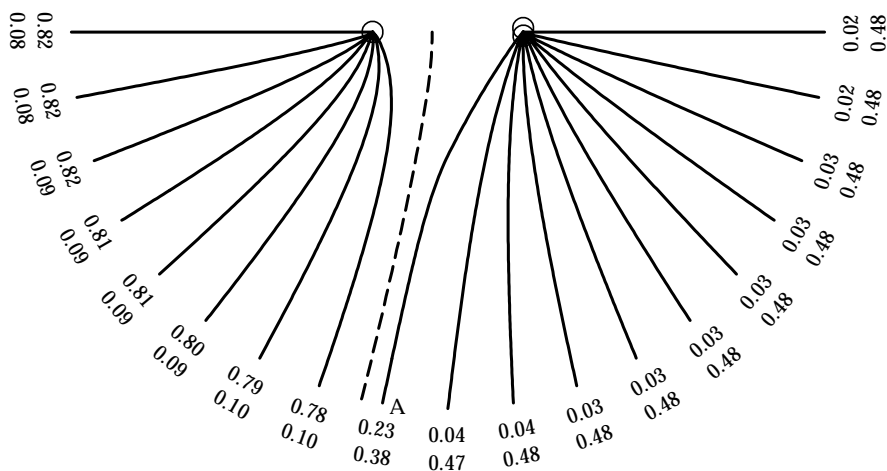


FIG. 5. Optimal trajectories (—) for different starting positions around a semicircle towards three targets (○). The two targets on the right are shown slightly apart but are in fact coincident; (---) separates the zones of attraction of the two target positions. The inner ring of numbers gives the probability of a hunter at that starting position reaching the solitary target. The outer ring gives the probability of reaching each of the two coincident targets. The mean rate of disappearance of each target is 0.1 per time taken to move a unit distance, where the target positions are 1 unit apart.

These zones of attraction are perhaps somewhat misleading, because when targets actually do disappear the target reached may not be the one in whose zone of attraction the hunter starts. So it is also meaningful to calculate the probabilities of reaching each target (for method, see the Appendix), and these are shown adjacent to the starting positions in Fig. 5. One use of these probabilities is to integrate them over an area around the targets and thus calculate an overall probability that one target is reached rather than another. This is the subject of Section 8 when I use such results to decide how targets should move to increase or decrease their probability of attracting optimal hunters.

Another informative analysis is to calculate the probability that all targets disappear before any of them are reached, in order to compare how well suboptimal policies perform relative to the optimal one. In Table 2 I consider the suboptimal policies of (a) moving straight to the nearest target, (b) following the steepest gradient [Fig. 6(a)], (c) using a triangle-of-forces calculation [Fig. 6(b)], and (d) moving straight to whichever position seems loudest [Fig. 6(c)]. Policies b, c and d assume that the hunter combines the signal from different targets additively, and thus two targets are more attractive than one, whereas policy a is unaffected by the number of targets at each

target location. Which suboptimal rules do best depends on the starting position, so the probabilities in Table 2 are averages over all starting positions within the semicircle shown in Fig. 6.

The right-hand column of Table 2 is the failure rate for each strategy. The optimal strategy has only a 1% lower failure rate than the strategy of going straight to the nearest or loudest target position, so these rules of thumb on average perform well. The gradient and triangle-of-forces

TABLE 2
The success/failure probabilities of optimal and suboptimal trajectories

Policy	Probability reach	Probability reach	Probability
	Target 1	Target 2	no target reached
Optimal	0.2763	0.2614	0.2009
Straight to nearest	0.2977	0.2499	0.2025
Steepest gradient	0.2803	0.2581	0.2035
Triangle-of-forces	0.2750	0.2605	0.2040
Straight to loudest	0.2598	0.2689	0.2024

Target 1 is at $(-0.5, 0)$, Targets 2 and 3 at $(0.5, 0)$. The rate of disappearance for each target is 0.5 per time taken to move 1 unit. Probabilities are averaged for 10^8 starting positions within the semicircle shown in Fig. 6 [<2.5 units from $(0, 0)$]. For each starting position I calculate the probabilities of reaching each target and of all targets having disappeared before any is reached. The probability of reaching Target 3 is identical to that for Target 2.

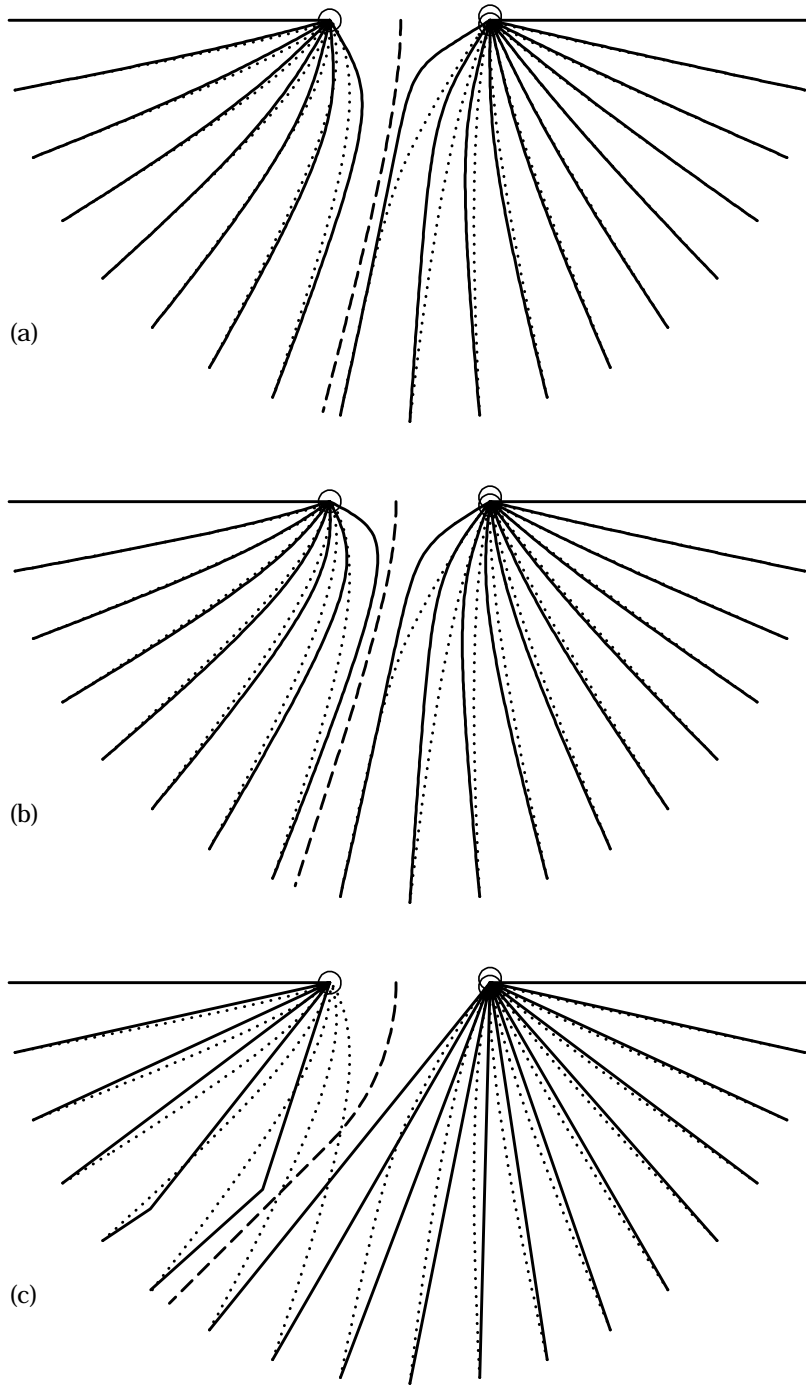


FIG. 6. Suboptimal trajectories (—) towards three targets (two coincident and one solitary). (a) Gradient rule; (b) triangle-of-forces rule; (c) straight-towards-loudest rule (in all cases assuming that signals from the three targets combine additively, and decay according to the inverse square law); (---) separates the zones of attraction of the two target positions; (⋯) are the optimal trajectories shown in Fig. 5.

strategies do slightly worse because they are too curved. However, these results depend on the disappearance probability and on the starting positions considered.

7. Experimental Evidence of Preference for Grouped Targets

The available data on the shape of trajectories allowed only a weak test of the

hypothesis. Another prediction to test is that hunters will head towards a group of two targets even if a solitary rival is closer. The dashed line in Fig. 5 sets a limit to how much further away the pair of targets can be before they should cease to be preferred. For a hunter starting on the straight line between the targets, the solitary target should be preferred if it is less than 0.66 to 0.67 as distant as the pair, but these values can rise to 1 if there is a high probability of interruption (or other extra time costs). For the suboptimal rules shown in Fig. 6 the corresponding values are 0.80 (gradient rule) and 0.71 (triangle-of-forces and straight-towards-loudest).

Unfortunately I know of no direct manipulations of the relative distances of the group and solitary caller from the hunter's starting position. Instead all that the available data test is the less critical prediction that when starting equidistant from the targets a hunter prefers the group. If a preference for groups is found there are numerous other explanations beside the one advanced here (review in Höglund & Alatalo, 1995, p. 168). Thus evidence that hunters prefer groups is merely consistent with my hypothesis. However, the evidence is worth examining because no preference for a group would refute the hypothesis for that species.

The best experimental evidence concerns frogs and insects where the male calls to attract a mate. Loudspeakers have been used experimentally to remove confounding factors present if real groups of males are used. Several studies have shown that females do prefer groups when the grouped and solitary loudspeakers are equidistant (e.g. Morris *et al.*, 1978; Cade, 1981; Walker, 1983; Schwartz, 1994), and Cade showed this also for a phonotactic parasitoid of a cricket. Other studies did not get a significant difference (Otte & Loftus-Hills, 1979; Shelley & Greenfield, 1991), and Telford (1985) clearly showed that his frogs preferred solitary loudspeakers.

8. The Stability of Groups of Targets

Now that we know for each starting point the probabilities that a hunter behaving optimally

will attain each target, we can determine how targets should space themselves. Prey should arrange themselves to minimise the probability of capture whereas males advertising for females should maximise this probability. The problem is game theoretic; the best position for one target will depend on the positions of its neighbours. The procedure that I use to test whether a particular arrangement of targets is an evolutionarily stable strategy (ESS) is to calculate an overall probability that hunters take a particular target, and then to ask whether a change in position of any one target increases or decreases the probability. This overall probability averages over different possible starting positions of the hunters.

8.1. RELATED WORK

Many benefits and cost of forming herds and leks have been proposed (reviews in Bertram, 1978; Wiley, 1991; Höglund & Alatalo, 1995), but there are two ideas in particular that are required for the interpretation of this paper's results. The first is termed attack abatement (Turner & Pitcher, 1986). The argument is that (1) if a predator is less likely to find a single group of prey than just one of the component prey items had they been scattered singly (the avoidance effect), and (2) if a predator attacking a group is less likely to catch a particular individual as group size increases (the dilution effect), then prey should form groups. The idea applies equally to females attracted to males, where it would normally select against leks forming. The opposite of the avoidance effect, the effect that a group of animals is easier to detect at a distance, has been used to explain leks; but it is generally implausible that the greater signal from a larger group outweighs the greater chance of encountering these individuals if they were dispersed (Bradbury, 1981). The hypothesis that I am testing here is also that groups of targets are more attractive, but not because they are easier to detect.

The other main geometrical argument is best known from Hamilton's classic paper on "Geometry for the selfish herd" (1971). This publicised a proposal of Williams (1964) that animals in groups shelter behind their neighbours. Animals on the edge of a group will be the

first that predators encounter and they gain less benefit from the group. But rather than dispersing they should try to get closer to the centre, and this process will thus make herds coalesce. Note that animals on the edge are sheltered on only one side, and whether this is a sufficient advantage to make an edge position preferable to being solitary depends on whether groups are more likely to be attacked than single individuals (Pulliam, 1973). Thus protection for individuals on the edge is only through attack abatement. As with attack abatement, the sheltering principle applies equally to leks, and makes them more difficult to explain.

8.2. METHODS

I examine the situation where one target leaves a group and I ask whether it is then more likely to be taken by a hunter moving optimally than if it had stayed in the group. This is similar to the approach of Cannings & Cruz Orive (1975) who examined several different movement rules of hunters, including the triangle-of-forces rule. Although this rule, like the optimal policy, means that groups of animals are more attractive than single individuals, Cannings & Cruz Orive concluded that groups are still stable if hunters are operating in two dimensions (although they used an approximation which is not valid if hunters can originate close to the targets). I take the group size including the leaver to be three, as this maximises the possibility that the leaver will attract fewer hunters than if it had stayed. The distance that the leaver moves away is envisaged as small: on average a hunter would have to traverse 20 times this distance before any particular target disappears.

A hunter is considered to notice the targets only if it lies within their "zone of influence". (This zone is a property of the group, in contrast with the term "zone of attraction" which describes movement towards a specified target.) In general we do not know from how far away hunters will be attracted to the targets and nor whether we should give more importance to hunters starting close to the targets that thus arrive early. So I ran the program with zones of influence of a series of different sizes. I also used two different configurations for the zones of influence, either overlapping circles of the same

radius centred on each target, or a single circle. In the former case a target leaving the group automatically gains hunters through extending the zone of influence to reach an unexploited market of hunters. In the latter case the centre of the circle is not moved when the target leaves, so that the zone of influence remains unaltered. The centre of this circle is put halfway between where the two target positions will be after the leaver has separated, which means that the leaver is in a similar position relative to the outline of the zone of influence both before and after it leaves. This procedure may seem somewhat unrealistic, but the aim was to eliminate the avoidance effect (Turner & Pitcher, 1986, discussed above); with the zone of influence fixed, any increase in the leaver's share of hunters cannot be through recruitment from a previously unexploited region.

I generate random starting positions within all squares of a fine grid and if a point is within the zone of influence I calculate the probabilities of a hunter reaching each target. These probabilities are calculated for over 5 million starting positions and Table 3 gives the averages. However, in the case when the leaver extends the zone of influence, all these probabilities are multiplied by the same factor as the increase in size of the zone of influence. So another way of viewing the figures is the expected number of hunters arriving at each target if the mean density of hunters is 1 per area of the original zone of influence (i.e. before the leaver separates).

For ease of calculation I assume that if the hunter is within the zone of influence of the group, it immediately is aware of all targets and continues to react to all of the surviving targets even if the only target within the critical radius disappears. All three targets are present when hunters start.

8.3. RESULTS AND DISCUSSION

The first column of figures in Table 3, for three coincident targets, shows that the expected number of hunters taking each target is, unsurprisingly, roughly one-third (a little less because sometimes the target has disappeared before a hunter arrives). The second column shows that, regardless of how we define the zone

TABLE 3
Does leaving a group increase the number of hunters attracted?

Zone of influence	Three targets coincident,		
	optimal = straight trajectory	Leaver separate, optimal trajectory	Leaver separate, straight trajectory
(a) Circle round each target, radius $2 \times$ separation of targets	0.333	0.547	0.623
(b) Circle round each target, radius $16 \times$ separation of targets	0.306	0.335	0.361
(c) Single circle, radius $2 \times$ separation of targets	0.333	0.402	0.478
(d) Single circle, radius $16 \times$ separation of targets	0.306	0.323	0.350
(e) Sphere round each target, radius $2 \times$ separation of targets	0.333	0.535	0.623
(f) Sphere round each target, radius $16 \times$ separation of targets	0.327	0.354	0.418

The expected number of hunters starting from within the zone of influence that reach the leaving target either before or after it has left a pair of similar targets. The figures are based on a density of hunters of 1 per area of the original zone of influence (i.e. before the leaver separates). When the three targets are coincident the hunters' optimal trajectories are straight lines. When the leaver has separated I give results both when the hunters take optimal curved trajectories and when they take suboptimal straight-line trajectories to the nearest target. The results depend on the size and shape of the zone of influence; intermediate sizes were also investigated and gave qualitatively similar results. The mean rate of disappearance for each target is 0.05 per time taken for a hunter to traverse the same distance as between the two target positions.

of influence, when the leaver separates it is more likely to attract a hunter. This implies that prey should not leave the herd and that males advertising for mates should disperse from a lek. If there were more than three targets the disadvantages to prey in dispersing, and to males in grouping, would be even larger (because the share of hunters before leaving is proportionately smaller).

The increase in the leaver's likelihood of attracting a hunter is larger when leaving increases the zone of influence (in Table 3 compare rows a and b with c and d). This is because the extension of the zone of influence is mostly in a region where hunters are much nearer the leaver than the group. This effect can be classed as a case of attack abatement (Turner & Pitcher, 1986). However, in reality a single individual might be less detectable than a group, so the solitary leaver might not distort the zone of influence in its vicinity as much. Nevertheless even with the effect of attack abatement removed (Table 3, rows c and d) the leaver gets more hunters. The reason for this is that the leaver puts itself nearer than the group to half the

hunters (the sheltering argument behind Hamilton's 1971 paper), and this outweighs its reduction in attractiveness compared with the group.

The increase in the leaver's likelihood of attracting a hunter is smaller when the zone of influence is larger (in Table 3 compare rows b with a, and d with c). This is because when the zone of influence is large, most hunters start from a long way off, and often in that case there are only two targets left by the time the hunter gets near, in which case its preference for a pair of targets over a solitary target cannot be expressed.

I have concluded that the increased attractiveness of a group cannot be an explanation of why leks form or herds split up. But a comparison of the second and third columns of figures in Table 3 shows that the leaver's increase in hunters is considerably less with the optimal trajectories than with the straight. So the advantages of forming a herd or splitting up from a lek are considerably less than we would suppose under the conventional assumption that hunters head straight to the nearest target. This quantitative

result is important because there are costs to living in herds (e.g. competition for food), and the reduction in benefits means that these costs might start to predominate. A tendency for hunters to bet-hedge might thus be a significant contributory reason for looser herds, or tighter leks.

9. Directions for Further Work

There are many ways in which this model may be extended and made more realistic—almost any of the assumptions listed in Section 3 could be violated. I now consider a few such modifications.

One assumption has been that the hunter is concerned to reach only one target. If targets could be taken one after the other, Fig. 3 shows that the trajectories should be less curved, particularly with low probabilities of disappearance. When there is a choice between a group of targets and a single target, the group should be an even better choice than when only one target could be taken.

I have assumed that hunters live on a two-dimensional surface, whereas aquatic and aerial species may occupy three dimensions. In the examples analysed above the targets are collinear, and in this special case the trajectories used in three dimensions are the same as in two. However, the extra dimension to the zone of influence makes a difference to the averaged probabilities of reaching each target. Lines e and f of Table 3 give the results for three dimensions: it still pays a prey item not to leave the group, but the cost of leaving is a little less. Note that Cannings & Cruz-Orive (1975) claimed that in the three-dimensional case, with hunters following the triangle-of-forces rule, grouping is neutrally stable; in fact, bearing in mind the approximation used, they should have concluded that targets now attract fewer hunters by leaving the group.

In many real examples hunters are competing with one another because it is only the first hunter to arrive that can eat the prey item or mate with the male. Finding the optimal trajectory is now much harder because the optimal trajectory of one hunter depends on the positions of its rivals, or, if these cannot be

directly observed, at least on the expected density of the rivals and on how long they have all been approaching the targets.

There are other reasons why policies of both hunters and targets should often depend on time as well as position. A group of targets occupying one position will steadily deplete the local supply of hunters, so at some stage it may be best for targets to move on. Similarly, since it takes time for females to approach, a male could be wasting his energy calling continuously because the audience has already heard his message. Indeed male frogs and crickets often call intermittently (e.g. Schwartz, 1994, and references therein). The optimal behaviour of hunters would have to adjust if targets can reappear as well as disappear: females might then continue to head towards a male that has fallen silent, but in other circumstances may switch direction towards a rival male that is still calling because they are more certain of the latter's continued presence. Models could get very complicated, but a message that I would emphasise is that in these situations optimal timing cannot be understood without an explicitly spatial perspective.

I have assumed that the hunters have complete knowledge of the presence and locations of all nearby targets. In fact our understanding of the sensory physiology of some phonotactic animals indicates that their knowledge is only partial. For instance the central nervous system of the bushcricket *Tettigonia viridissima* transmits only the loudest sound source at each of its ears (Römer, 1993). One way to elaborate my model would be to incorporate such constraints; different decision rules and trajectories will result but the advantages in bet hedging will still influence what parameter values are optimal. Another way of saying this is that some rules of thumb will perform better than others, as this paper has demonstrated.

Lastly I would emphasise that I believe that my models are testable empirically. In situations where targets disappear unpredictably, do hunters really bet hedge by taking curved trajectories and do they prefer groups? The theoretical results suggest that the advantage for them to do so, whilst not negligible, is not great. In my own behaviour in everyday life and on the sports field I know that I

personally do take bet-hedging trajectories, but I hope that someone can demonstrate some other examples.

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APPENDIX

A1. Backwards Problem

Consider initially that there are just two targets, T1 and T2, at positions (x_{T1}, y_{T1}) and (x_{T2}, y_{T2}) . They disappear at a mean rate of p_{T1} and p_{T2} , and have a value to the hunter of v_{T1} and v_{T2} . The expected reward of a hunter at position (x, y) when both targets are available is written as $R_{11}(x, y)$, when only the first remains as $R_{10}(x, y)$, when only the second remains as $R_{01}(x, y)$. The hunter gets no reward if no targets remain, so $R_{00}(x, y) = 0$. $R_{01}(x, y)$ and $R_{10}(x, y)$ are easy to calculate because the optimal trajectory when only one target remains is clearly a straight line and we merely need to calculate

the probability that the target survives until the hunter arrives. Assuming that hunters move 1 unit in 1 time interval,

$$R_{10}(x, y) = v_{T1} \exp(-p_{T1} \sqrt{(x_{T1} - x)^2 + (y_{T1} - y)^2}).$$

$R_{11}(x, y)$ can only be written down in terms of the expected rewards at adjacent points. Consider that the hunter is at position (x, y) and is about to make a small straight-line step of length s in direction θ to $(x + s \cos \theta, y + s \sin \theta)$. While making this step, none, either, or both of the targets may disappear, so the expected reward is a sum of the expected rewards when each possible combination of targets is still present, weighted by the probability of the relevant targets having, and not having, disappeared.

$$\begin{aligned} R_{11}(x, y) &= R_{11}(x + s \cos \theta, y + s \sin \theta) \\ &\quad \times \exp(-s(p_{T1} + p_{T2})) \\ &+ R_{10}(x + s \cos \theta, y + s \sin \theta) \\ &\quad \times \exp(-sp_{T1})(1 - \exp(-sp_{T2})) \\ &+ R_{01}(x + s \cos \theta, y + s \sin \theta) \\ &\quad \times (1 - \exp(-sp_{T1}))\exp(-sp_{T2}) \quad (\text{A.1}) \end{aligned}$$

We already know the R_{10} and R_{01} terms. $R_{11}(x + s \cos \theta, y + s \sin \theta)$ has to be interpolated from R_{11} at adjacent points, as I explain presently.

I use the technique of dynamic programming (McNamara & Houston, 1986; Mangel & Clark, 1988). Its essential principle is to work backwards in time one step at a time, at each step optimising the decision given the expected rewards one step in the future. Its application to two-dimensional spatial problems proved not completely straightforward.

First a grid of points is superimposed onto the landscape. For simplicity I position targets on grid points. For grid points on which a target lies we immediately know that the expected reward is v_{T1} or v_{T2} [Fig. A1(a)]. I then estimate the expected reward at the four nearest grid points around each target [Fig. A1(b)]; I use eqn (A.1) and assume that it is optimal to travel straight to this target ($s = 1$, $\theta = 0, \pi/2, \pi$ or $3\pi/2$). From now on, however, the optimal direction is

calculated by finding the value of θ that maximises the quantity in eqn (A.1), given that the step size $s = 1$. The $R_{11}(x + s \cos \theta, y + s \sin \theta)$ term is estimated by interpolation from adjacent points at which R_{11} has already been estimated. Thus for the grid point $(x_{T1} - 1, y_{T1} - 1)$ diagonally adjacent to target T1, $R_{11}(x_{T1} - 1 + \cos \theta, y_{T1} - 1 + \sin \theta)$ is interpolated from the values of $R_{11}(x_{T1}, y_{T1})$, $R_{11}(x_{T1} - 1, y_{T1})$, and $R_{11}(x_{T1}, y_{T1} - 1)$, which are the nearest grid points if $0 \leq \theta \leq \pi/2$. By finding the value of θ that maximises the quantity in eqn (A.1), we simultaneously find the optimal policy (direction to move) and the expected terminal reward at (x, y) under the optimal policy (the quantity maximised). Thus by working outwards from points where the expected reward is already estimated I can estimate the expected reward at adjacent points. Eventually the region for which there are these estimates spreads over the whole grid (Fig. A1).

In fact I could have found these points analytically up until the stage when the region of estimates around one target expands to overlap the region of estimates around another target [Fig. A1(f)]. Until then the optimal policy should be to head straight for the nearest target. After that the optimal policy and R_{11} are influenced by the position of both targets (which is the whole point of the model). Consequently the optimal policy and R_{11} at each point has to be recalculated many times as the R_{11} of the neighbouring points also change; the process continues until successive iterations make little or no difference to any of the values.

To my surprise it proved absolutely vital to use quadratic, rather than linear interpolation to calculate R_{11} . (In fact I use quadratic interpolation on the logarithm of R_{11} .) Consequently R_{11} is influenced by five points in any quadrant, and these five points will be different when evaluating θ in different quadrants around each point. The problem with using linear interpolation is that it leads to false optima near the transition from one quadrant to another (when the points used for the interpolation change). I instead tried fitting two-dimensional cubic splines over the whole grid, but without success.

Unfortunately, when searching for θ that maximises expected reward there will often be

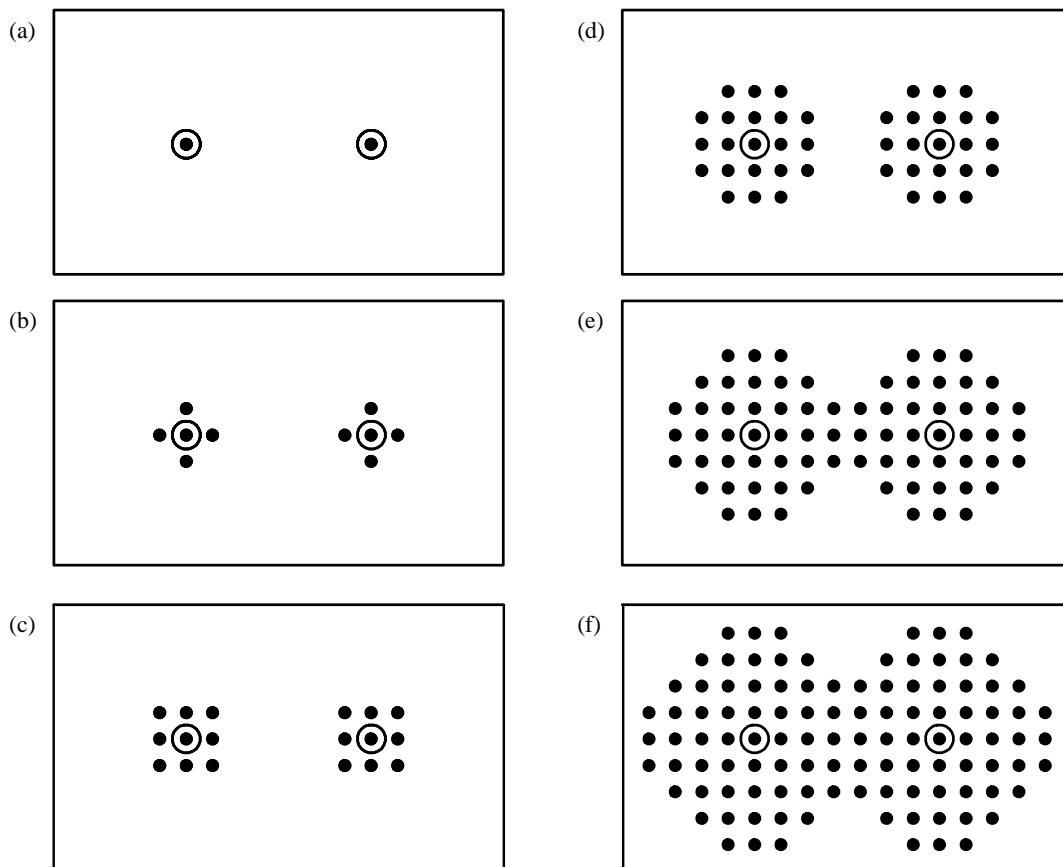


FIG. A1. (a) to (f) show successive stages of the dynamic programming. The two \odot indicate target positions; \bullet indicates that the expected terminal reward and optimal direction have been estimated for that grid point.

several local optima (each usually corresponding to heading in the rough direction of each of the targets). It is not sufficient therefore merely to use hill-climbing techniques, such as Newton's method, to find the optimal θ in each quadrant. Instead I initially test a range of values of θ (every degree or finer); then, starting at the value of θ that yielded the largest R_{11} , I use Newton's method to locate the optimum more precisely.

We expect the optimal policy to be to head somewhere between the targets, or straight towards a target, but never away from all targets. For many grid points, therefore, I can restrict the values of θ searched. Where possible I place the grid so that the targets all have the same value of y . I can then make use of the symmetry and analyse a grid only half the size.

With three targets, the equivalent of eqn (A.1) is more complicated as we need to calculate R_{111} , which is the weighted sum of R_{110} , R_{101} , R_{011} , R_{100} , R_{010} and R_{001} . Thus first it is necessary to work out the optimal policies and expected rewards

when each possible combination of just two targets survive (i.e. R_{110} , R_{101} , R_{011}). Once these values are known it is possible to work out R_{111} . Similarly one could build up to coping with more targets.

Despite much involved book-keeping to reduce the amount of calculation, finding the optimal solutions over a 200 by 100 grid even in the two-target case takes of the order of an hour on a SUN workstation.

A2. Forward Problem

Having found the optimal policy (direction) over the whole grid I can now run forward in time to calculate optimal trajectories. The procedure is simply to move one unit in the optimal direction and then recalculate the optimal direction at the new location. Generally the new location will not be on a grid point so that the direction is interpolated from directions at the adjacent grid points.

With two targets, and with particular arrangements of more targets, there is a potential problem at points symmetrically placed with respect to the targets. The optimal policy is to go either left or right. Isaacs (1965) calls such lines dispersal surfaces. Careful programming is required to flag such situations, otherwise one of the targets will end up with an unfair share of hunters.

A related, and more troublesome, problem is that interpolating optimal directions from a set of grid points lying both sides of a dispersal surface should be avoided (averaging a left and a right turn results in the suboptimal policy of moving parallel to the dispersal surface); instead it is necessary to extrapolate from grid points on the same side of the dispersal surfaces. In simple cases this is achievable by recognising the line of symmetry *a priori*. In more complex cases an effective (but not infallible) method to recognise points lying on different sides of the dispersal surface is to test whether the trajectories from them lead to the same target if there happen to be no disappearances (for this preliminary calculation interpolation across the unrecognised dispersal surfaces will occur). A cruder approach is simply to make the grid finer, which decreases the proportion of interpolations that are inappropriate.

From the optimal directions calculated at each grid point it is thus possible to calculate an optimal curved trajectory starting from any point. One can either assume that no disappearances actually happen to occur, or use random numbers to simulate trajectories in which targets do disappear with their prescribed probabilities, so that the trajectories show sudden switches of direction.

Averaging the outcomes of many such simulations would estimate the probability of each target being attained from a given starting position. However, I use a more efficient method to calculate these probabilities. Suppose that out of three targets only Target 3 remains. The optimal trajectory from any point (x, y) is then a straight line and it is straightforward to calculate the probability that Target 3 still remains by the time the hunter reaches its position; call this $P_{[3|001]}(x, y)$. What I want to calculate eventually is $P_{[1|111]}(x, y)$, $P_{[2|111]}(x, y)$ and $P_{[3|111]}(x, y)$, the probabilities that each target

is attained given that when the hunter was at (x, y) all three targets were present.

The first step is to calculate and store values of $P_{[1|100]}(x, y)$, $P_{[2|010]}(x, y)$ and $P_{[3|001]}(x, y)$ for all x, y . Then I consider the situation when two targets remain, and follow the optimal trajectory from each point when no disappearances happen to occur. Along this trajectory I calculate the probability that each target disappears between the successive interpolations of a new direction. The probability that over a distance D Target 3 disappears and Target 2 survives when only Targets 2 and 3 remain at the start is written $Q_{[011 \rightarrow 010]}(D)$. If Target 3 does disappear the trajectory will change to a straight line, and one can then calculate the probability that the remaining Target 2 will not have disappeared by the time it is reached. Rather than calculate this directly, however, I interpolate it from the stored table of $P_{[2|010]}(x, y)$. The technique is to work along the optimal trajectory when no disappearances happen to occur, keeping a running score of the probabilities that each target is the destination if a disappearance were to occur.

$$\begin{aligned} P_{[2|011]}(x_i, y_i) &= Q_{[011 \rightarrow 010]}(D_i)P_{[2|010]}(x_{i+1}, y_{i+1}) \\ &\quad + Q_{[011 \rightarrow 011]}(D_i)P_{[2|011]}(x_{i+1}, y_{i+1}) \\ \Rightarrow P_{[2|011]}(x, y) &= \sum_{i=0}^N Q_{[011 \rightarrow 010]}(D_i)P_{[2|010]}(x_{i+1}, y_{i+1}) \\ &\quad + P_{[2|011]}(x_N, y_N) \prod_{i=0}^N Q_{[011 \rightarrow 011]}(D_i) \end{aligned}$$

where $D_i =$ distance between (x_i, y_i) and (x_{i+1}, y_{i+1}) , and $P_{[2|011]}(x_N, y_N)$ is 1 or 0 depending on whether Target 2 is the end-point of the optimal trajectory from (x, y) if there happen to be no disappearances.

Having calculated the probabilities that each target is attained given each possible combination of two targets remaining at the start, one can then use the same principles to calculate these probabilities given that all three targets remain at the start. Now it is even more important that one can follow a single trajectory and calculate the consequences of a disappearance by interpolation from a table, rather than by having to follow the innumerable possible branches of the trajectory.