

Patch choice under perceptual constraints: a cause for departures from an ideal free distribution

Mark V. Abrahams

Biological Sciences Department, Simon Fraser University, Burnaby, British Columbia, V5A 1S6, Canada

Received January 25, 1986/ Accepted July 20, 1986

Summary. A review of tests of ideal free distribution (IFD) theory reveals a characteristic bias: patches with a small proportion of the resources are relatively overused and patches with a larger proportion of the resources are relatively underused. A model is developed to examine how animals with limited abilities to perceive differences in patch quality affect an IFD by foragers. This constraint produces the observed bias, a bias that is exaggerated as the number of patches increases. Sutherland (1983) has developed a model based on interference which can also explain the observed bias. The two models can be differentiated in that only the perception limit model (this paper) is sensitive to absolute changes in overall resource availability and to increases in the number of animals. Additionally, Sutherland's model predicts that when deviations away from an IFD occur there will be no differences in intake rates, while the perception limit model predicts that intake rates should vary between patches.

Introduction

The ideal free distribution (IFD) theory was developed by Fretwell and Lucas (1970) and Fretwell (1972) to describe how animals should distribute themselves within an environment between patches of varying suitability. If patch suitability declines as the density of animals in that patch increases, the IFD predicts that the proportion of animals in a patch will equal the proportion of resources available in that patch. For such a situation to occur, all animals must be 'ideal' in their ability to select a patch which maximizes fitness (they must have perfect information about the environment) and be 'free' to enter and use any patch

on an equal basis with other residents (all animals must be identical with respect to their competitive abilities).

In systems where patch suitability can be determined, IFD theory can be used to predict animal distributions. Published studies have fallen into two major categories: animals competing for breeding opportunities (Parker 1978; Davies and Halliday 1979; Courtney and Parker 1985; Sargent et al. 1986) and animals competing for food (Milinski 1979, 1984; Zwarts and Drent 1981; Harper 1982; Sutherland 1982; Talbot and Kramer 1986; Godin and Keenleyside 1984; Power 1984; Gillis 1985). These experiments record data in either spatial or temporal form. The spatial experiments record the proportion of resources in a patch and the proportion of animals using those patches. In these studies a characteristic bias has been observed: patches which have a small proportion of the resources have disproportionately more individuals using them and conversely, patches with a large proportion of the resources are underused (Table 1). In addition, Sutherland (1982) noted in his field observations of oystercatchers (*Haematopus ostralegus*) that too many individuals used poor patches than would be predicted by an IFD.

The temporal experiments record the distribution of animals through time between two non-depleting patches. These experiments also exhibit a bias towards overuse of poor patches (Table 2). Further, since all experiments contained only two patches the most profitable patches had fewer animals than predicted.

Some authors have observed that their animals were not all of equal competitive ability and hypothesized that the observed deviation resulted from a violation of the 'free' assumption (called an ideal despotic distribution, Fretwell 1972). However, Milinski (1984) could find no effect of

Table 1. Departures from an IFD for spatial data, which illustrate the characteristic overuse of poor patches and underuse of good patches. A good patch contains an above average proportion of resources and a bad patch contains a below average proportion of the resources. A study is considered to show evidence of a bias when greater than one half of the observations deviate in one direction from the predicted result. Numbers in parentheses represent the sample size

Data source and species	Proportion of observations greater than expected on poor patches	Proportion of observations less than expected on good patches
Courtney and Parker (1985) Figs. 5, 9 and raw data <i>Tarucus theophrastus</i>	0.76 (37)	0.77 (35)
Davies and Halliday (1979) Fig. 13 <i>Bufo bufo</i>	0.60 (5)	0.75 (4)
Gillis (1985) Fig. 3 30 fish	0.33 (6)	0.33 (3)
Fig. 3 60 fish	0.83 (6)	0.67 (3)
Fig. 3 120 fish	1.00 (6)	1.00 (3)
Fig. 3 240 fish <i>Brachydanio rerio</i>	0.67 (6)	1.00 (3)
Parker (1978) Fig. 8.3 <i>Scatophaga stercoraria</i>	1.00 (2)	1.00 (3)
Sargent et al. (1986) Fig. 2a 1981 data	0.80 (10)	0.73 (11)
Fig. 2b 1982 data <i>Oncorhynchus kisutch</i>	0.67 (6)	0.50 (6)
Talbot and Kramer (1986) Fig. 2 <i>Poecilia reticulata</i>	0.73 (15)	1.00 (10)
Zwarts and Drent (1981) Fig. 6 Low density	0.86 (7)	0.88 (8)
Fig. 6 High density <i>Haematopus ostralegus</i>	0.83 (6)	0.88 (8)
Total greater than 0.5	11	10
Total	12	12
Proportion	0.92	0.83

unequal competitive abilities on an IFD in sticklebacks (*Gasterosteus aculeatus*). Godin and Keenleyside (1984) also observed no significant differences in intake rates of animals within a patch which might have indicated despotic behaviour and a violation of the 'free' assumption. Therefore, basing explanations of deviations from an IFD upon despotic behaviours may not always be warranted.

Unequal competitive abilities may cause deviations from an IFD by a mechanism other than despotic behaviour. Sutherland and Parker (1985)

Table 2. Departures from an IFD for temporal data, which illustrate overuse of poor patches. These studies examine single distributions with multiple observations at predetermined points in time. Again, an overbias occurs when greater than one half of the observations are greater than predicted by an IFD. Data represent the mean results of multiple observations taken only when the distribution reached an equilibrium. If a dynamic stage existed in the distribution, it was excluded by fitting a straight line to the initial points of the distribution. The point at which observations did not conform to this line was considered to be the beginning of the equilibrium distribution

Data source and species	Data from least profitable patch		
	Ratio	Proportion of observations greater than expected	<i>n</i>
Godin and Keenleyside (1984) Fig. 2	2:1	0.61	28
Fig. 2 <i>Aequidens curviceps</i>	5:1	1.00	25
Harper (1982) Fig. 2 <i>Anas platyrhynchos</i>	2:1	0.50	12
Milinski (1979) Fig. 1	5:1	0.71	28
Fig. 2	2:1	1.00	15
Fig. 2 <i>Gasterosteus aculeatus</i>	2:1	1.00	13
Milinski (1984) Fig. 3	2:1	0.44	16
Fig. 3 <i>Gasterosteus aculeatus</i>	2:1	0.38	16
Total greater than 0.5		5	
Total		8	
Proportion		0.625	

and Parker and Sutherland (1986) argue that in experiments with a continuous-input of resources, unequal competitive abilities will result in animals distributing themselves such that the sum of competitive abilities will conform to the predicted distribution of an IFD. If the animals are not all of equal competitive ability, the distribution of animals will not necessarily conform to an IFD. This mechanism does not predict a specific deviation from an IFD and as such would not predict the consistent overbias observed in the literature.

Sutherland (1983) has suggested in situations where there is no continuous-input, as in most field observations, deviations from an IFD could be due to interference. In Sutherland's model, interference is considered to be any kind of interaction between predators which reduces searching efficiency. This is distinct from despotic behaviour in that all ani-

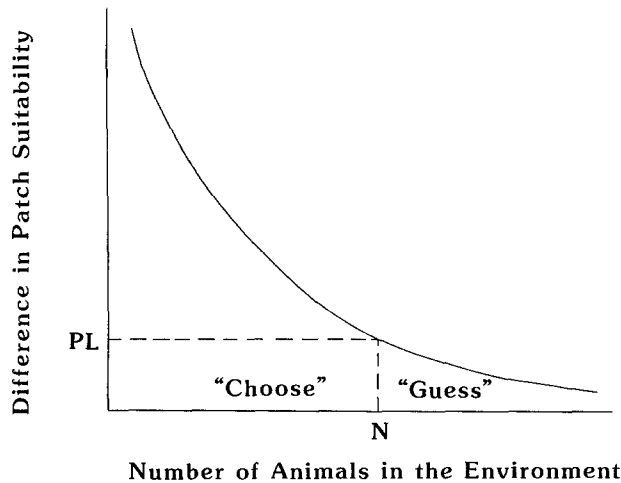


Fig. 1. The relationship between the difference in patch suitability and the number of animals in the environment. If a limited ability exists to resolve differences between patch suitabilities (PL) then only a limited number of animals (n) will be able to choose which patch to enter. All animals beyond this point will be unable to resolve differences in patch suitability and will have to choose a patch at random (“guess”)

imals within a patch are affected equally; despotic behaviour results in unequal use of resources by individuals within a patch. Sutherland’s (1983) model assumes that interference will cause patch suitability to decline more rapidly with increases in animal density than would be predicted by an IFD. Therefore, the deviation from an IFD may be due solely to errors in perspective, with the observer overestimating patch suitabilities at high densities in comparison to their actual value to the animal. What appears to the observer as a departure from an IFD may actually be a perfect IFD from the animals’ perspective.

This paper presents an alternative model to examine departures from IFD’s based on limited perceptual abilities. It examines the predicted results of an IFD experiment when animals have a limited ability to resolve differences in patch suitability while foraging for food.

Methods

In designing this model I assumed that animals assess patch suitability from perceived individual intake rates, not from the total amount of food available in the patch (see Harper 1982; Milinski 1984). Hence, the quality of a patch is equal to the total amount of food available (F) divided by the total number of animals in the patch (n) plus the animal which is making the decision whether or not to enter or stay in that patch, i.e. patch suitability equals $F/(n+1)$.

A consequence of animals assessing patch suitability in this manner is that the difference between any two patches will be greatest at the lowest total densities of predators. The effect of animals preferentially going to the best patches, thereby re-

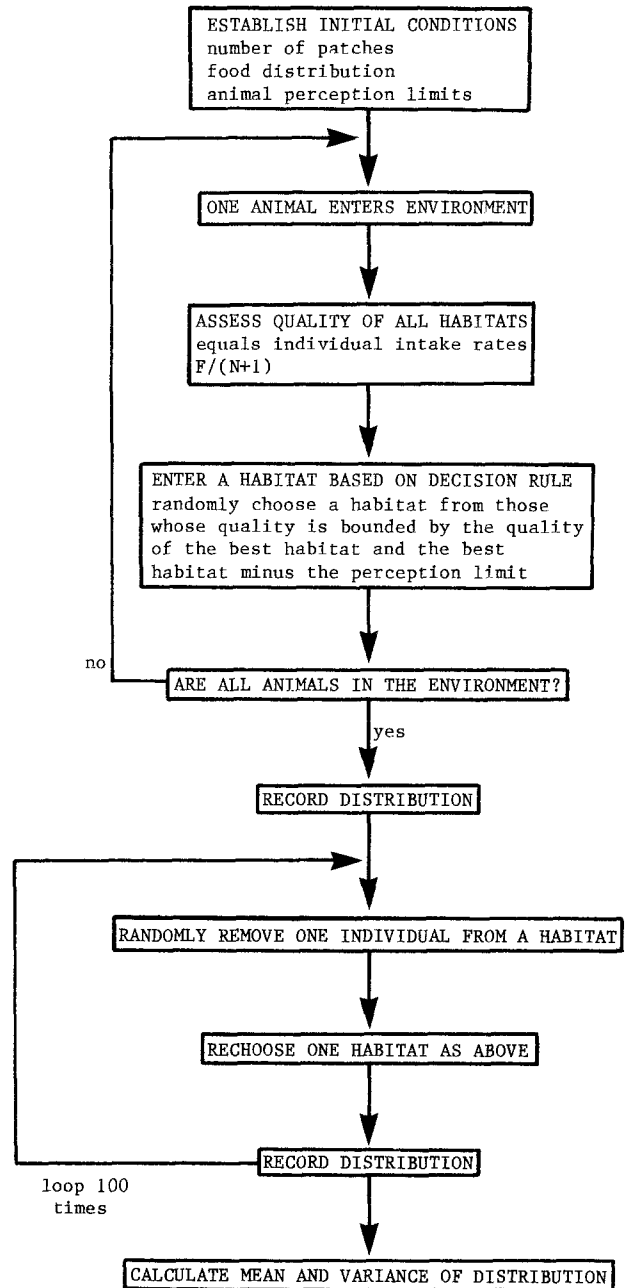


Fig. 2. Flowchart illustrating model operation. See text for details

ducing their suitability, will lower the absolute difference between patches. As a result, with a fixed food supply the differences between patches will decrease asymptotically as the number of animals in the environment increases (Fig. 1).

If animals are ‘ideal’ they will be unaffected by this decay function. However, if there is some finite level beyond which differences in patch suitability cannot be resolved (a perception limit), then those animals entering after this point will be unable to gain sufficient information to choose the most profitable patch (Fig. 1).

The initial condition of the model (Fig. 2) was an environment containing an undepletable food supply available at a rate of 20 food units per unit time, distributed between two, three, or four patches. Simulations were performed in situations

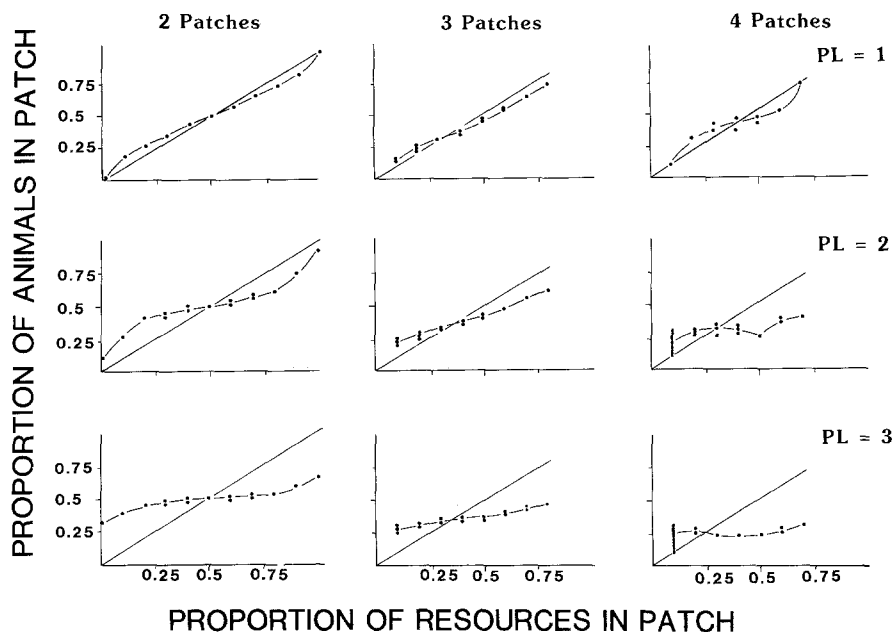


Fig. 3. Results of simulations for three different perception limits (PL) of animals in an environment with the resources distributed between two, three or four patches. The *diagonal lines* represent the distribution predicted by IFD, the *curved lines* are interpolations of the simulated distributions

where the food was divided between patches in such a way that no patch contained less than two food units.

The model operated by sequentially entering 10 animals into the environment. Every animal was identical, i.e., they were each capable of consuming all the food by themselves, they had the same perception limit (they were able to perceive differences in patch quality of one, two, or three units of food per unit time per individual), and they all used the same decision rule. The decision rule was simply to go to the best patch when that could be perceived. If the best patch could not be resolved from the next best patch due to the difference in suitability being less than the perception limit, one of the indistinguishable patches was chosen at random. In a multi-patch system, as the perception limit increases, or patch suitabilities become more similar, the animal must choose randomly between an increasing number of patches. This decision rule can most easily be explained by a numerical example. Consider an animal entering an environment with four patches which have patch suitabilities of 3.5, 2, 1.4 and 1. If the animal has a perception limit of one it will correctly enter the patch with the highest suitability. However, if the perception limit is two the animal will be unable to perceive differences between 3.5 and anything greater than 1.5 and will have to choose randomly between the two best patches. As the perception limit increases the probability increases that an animal will have to choose a patch randomly (henceforth referred to as guessing).

After an initial distribution was determined, the animals were allowed to redistribute. This is analogous to switching, which has been observed in IFD experiments (Milinski 1979; personal observation). Individuals were chosen randomly to vacate a patch (causing an adjustment in the rate of food availability) and to rechoose a patch using the original decision rule. One hundred resamplings were allowed.

Data were recorded on the position of the animals for each of the 100 resampling periods and the final result obtained was the overall average. The simulation was run 10 times for each distribution of food and perception limit and the mean and variance of the distributions was recorded.

The deviations from an IFD produced by this model were compared to the predictions of Sutherland's (1983) model to

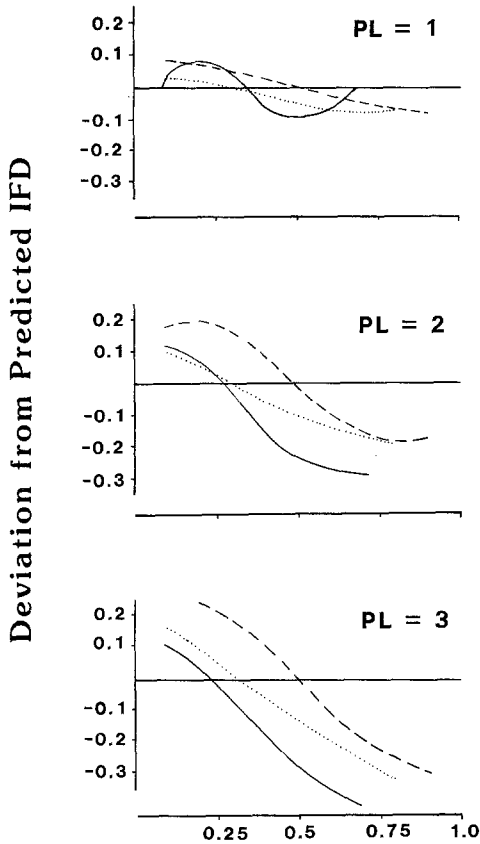
determine if they could be distinguished quantitatively. The predicted IFD distributions from Sutherland's model are generated by the equation $B_i = ca_i^{1/m}$ where B_i is the proportion of animals in the i th patch, a_i is the proportion of resources in the i th patch, m is the degree of interference and c is a normalizing constant such that the B_i values sum to unity.

Results

The results of the simulation are illustrated in Fig. 3. The most striking result of this simulation is that any deviation from perfect information will produce only one type of bias, an underuse of good patches and an overuse of poor patches.

The size of the deviation is affected by the perception limit. As the deviation from an IFD increases, so do the differences in individual intake rates. Since animals choose patches upon the basis of individual intake rates, any deviation which exceeds their perception limit will provide enough information for the next animal to choose the correct patch. Therefore the perception limits provide feedback which limit the difference in individual intake rates and the magnitude of the deviation from an IFD.

Two opposing forces affect the shape of the distribution. As the environment becomes less uniform, the initial differences in patch suitability increase and the number of animals which must guess is reduced. This provides a force limiting the deviation from an IFD at extreme resource distributions. However, since guessing distributes the animals in a uniform manner, guessing animals are "more wrong" at less uniform resource distribu-



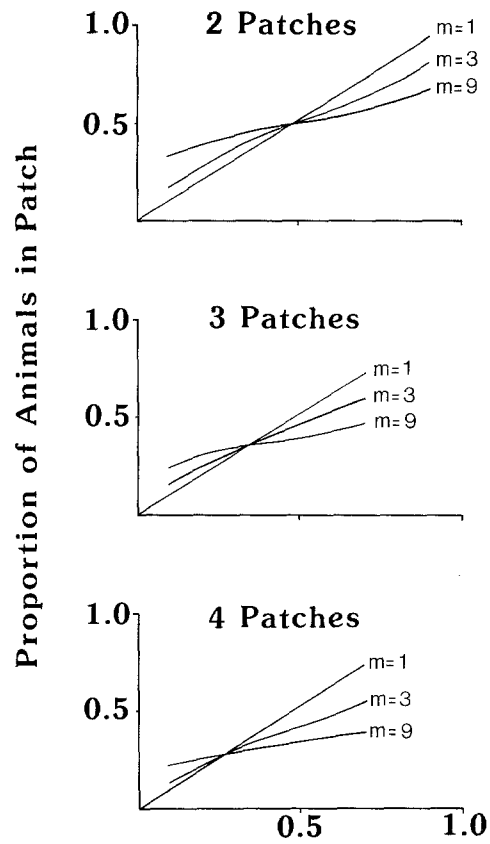
Proportion of Resources in Patch

Fig. 4. The biases produced from an IFD as a result of the combined effects of varying abilities to perceive differences in patch suitability (PL) and the number of available patches. The deviation corresponds to the observed distribution minus the predicted distribution. *Solid lines* represent four patch systems, *dotted lines* three patch systems and *dashed lines* two patch systems

tions. This provides a force producing less deviation at a uniform resource distribution. A consequence of these conflicting forces is a smaller deviation from an IFD at extreme resource distributions with good perception limits (PL=1, Fig. 4). However, this trend does not continue as PL increases (PL=2 and 3, Fig. 4), because the large differences in patch suitability are no longer great enough to be perceived and the number of guessers is no longer reduced. Therefore the inefficiency of guessing causes the deviation to increase at extreme resource distributions.

Perception limit model vs Sutherland's model

Sutherland's (1983) interference model produces approximately similar dynamics to this model when large m values (levels of interference) are used (maximum m value from the literature is 1.13)



Proportion of Resources in Patch

Fig. 5. Predicted distributions from Sutherland's (1983) interference model for three different interference levels (m)

(Fig. 5). However, there are some subtle differences between the models. Sutherland's model predicts an increasing deviation away from the IFD at extreme differences in patch suitability. In addition, the inflection point (by definition the point which divides patches into good and bad) is constant for all levels of interference: in all cases it is equal to the reciprocal of the number of patches in the environment. The inflection point in the perception limit model is affected both by the number of patches in the environment and the perception limit, and ranges between 1/2 and the reciprocal of the number of patches. This is because the type of guess an animal makes is a function both of the number of patches available and the number which are indistinguishable as the 'best' patch. For example, when there are four patches in the environment, the inflection point shifts towards the origin (Fig. 4). At low perception limits an animal may only have to guess between two indistinguishable patches, but as the perception limit increases more patches will become indistinguishable from the best patch.

Another distinction which is inherent in the assumptions of the two models is that net intake rates will not differ between patches when the bias is produced by interference. However, the perception limit model predicts that the resource will be used inefficiently such that individuals in a high quality patch will have a greater intake rate than those in the poor patches, the degree of this difference not exceeding individual perception limits.

Discussion

The simple and reasonable assumption that animals are constrained by some finite level at which differences in patch suitability can be perceived produces a characteristic bias from an IFD. This bias is a result of the random patch choice rule used when differences cannot be perceived between patches. Since the rule states that any indistinguishable patch is chosen with equal probability, too many animals will go to a poor patch and too few to a good patch. However, the extent of this bias will be regulated by the perception limit. If the deviation from an IFD becomes very large, the difference in patch suitability will again become perceptible resulting in those animals who enter the environment later (or those who resample) choosing the best patch and reducing the deviation. As a result, deviations from an IFD by a perception limit should produce a stable, characteristic distribution.

Since the shape of the deviation from an IFD with a random decision rule closely resembles the results of Sutherland's (1983) interference model, distinguishing the cause of the bias would not be possible solely from the results of field observations on distributions. Indeed, since the two models violate different assumptions of the IFD (the interference model affects availability of resources while the perception limit model affects abilities to perceive relative levels of availability of these resources) it is possible for both to operate simultaneously.

However, the two hypotheses can be distinguished by experimental manipulation. The perception limit model predicts that any manipulation which increases the proportion of animals which must guess which patch to use will increase the deviation away from an IFD; Sutherland's model predicts that deviations are solely dependent upon the interference level. Therefore, the perception limit model predicts that decreasing the overall resource density without changing proportions available in each patch will increase the deviation from an IFD whereas Sutherland's model predicts

no change. The perception limit model also predicts that increasing the number of animals in the environment will increase the deviation from an IFD whereas Sutherland's model predicts no change with a constant interference level.

The two hypotheses may also be distinguished a posteriori if data are available on net individual intake rates. If a deviation from an IFD is observed, the perception limit model would predict that individuals in good patches will have greater net intake rates than individuals in poor patches. Sutherland's model would predict no differences in net individual intake rates between patches assuming all animals are identical.

In this model, the environment was assumed to be deterministic such that no new information was required once the distribution was known. However, recent attention has been given to the cost of acquiring information in a stochastic environment (see Kacelnik and Krebs 1985 for a brief review). In a previous model, Regelman (1984) used a learning rule which generated a similar effect to this model. Rather than examining the population, as in this model, this rule was used to describe decisions made by each individual at a given point in time. In this model, each individual chooses a patch based upon the ratio of patch profitabilities incorporating both current and past rewards with either a cost or no cost to switching patches. This model resulted in more individuals in the poor patch than predicted by an IFD and was attributed to all individuals having an equal probability of resampling the environment. Since there are more individuals in the better patch, the probability of more individuals moving from the best to the worst patch are greater than vice versa. This effect was more profound when a cost was associated with switching patches.

The mechanism which results in the overuse of the poor patch in this model results from the random nature in which animals' make decisions when there is no perceived difference in only the current value of the patches. If patches are not perceived to be different it is assumed that they are of equal value. Thus, too many animals appear in the poor patch because the random decision rule distributes animals in a characteristic deviation from an IFD. This is distinct from patch choice by animals in Sutherland's model since interference produces real differences in patch quality to animals which must compete for food.

Since deviations from an IFD increase with the number of simultaneous choices an animal must make, the effect of a finite perception limit will become more obvious in complex environments.

The result will be an inefficient use of the available resources. Rules of thumb used by animals to benefit from this deviation (eg. if patch difference is not perceptible, go to the patch with the greatest number of competitors) will not spread as their benefits are inversely proportional to their frequency in the population. From a game theory point of view, the population is not displaying an evolutionarily stable state (Maynard Smith 1973) and therefore should be susceptible to invasion by a mutant with a greater ability to resolve patch differences. That deviations from IFD's exist in observed distributions suggests either that the population is still evolving improved perception limits, or that the benefit gained from improved perception limits would be offset by the increased cost of gaining information. If the latter is the case, deviations from an IFD in the absence of interference represent the equilibrium point between the benefits of improved information and the cost of achieving these benefits.

Acknowledgements. R. Cartar, L. Dill, D. Gillis, M. Gross, D. Kramer, G. Martel, P. Nonacs, C. Sargent, R. Ydenberg and two anonymous referees kindly commented on earlier drafts of this manuscript. Thanks go to S. Courtney for providing raw data from his paper for Table 1. Financial support during this research was provided by an NSERC postgraduate scholarship, a graduate research fellowship from Simon Fraser University, and NSERC Canada Grant A6869 to L. Dill.

References

- Courtney SP, Parker GA (1985) Mating behaviour of the tiger blue butterfly (*Tarucus theophrastus*): competitive mate-searching when not all females are captured. *Behav Ecol Sociobiol* 17:213–221
- Davies NB, Halliday TR (1979) Competitive mate searching in male common toads, *Bufo bufo*. *Anim Behav* 27:1253–1267
- Fretwell SD (1972) Populations in a seasonal environment. Princeton University Press, Princeton
- Fretwell SD, Lucas Jr. HL (1970) On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor* 19:16–36
- Gillis DM (1985) Animal aggregation, interference and the ideal free distribution, M Sc thesis, McGill University, Montreal P.Q., p 60
- Godin J-GJ, Keenleyside MH (1984) Foraging on patchily distributed prey by a cichlid fish (Teleostei, Cichlidae): a test of the ideal free distribution. *Anim Behav* 32:120–131
- Harper DGC (1982) Competitive foraging in mallards: 'ideal free ducks'. *Anim Behav* 30:575–584
- Kacelnik A, Krebs JR (1985) Learning to exploit patchily distributed food. In: Sibly RM, Smith RH (eds) *Behavioural Ecology: Ecological consequences of adaptive behaviour*. Blackwell Scientific Publications, Oxford, pp 189–205
- Maynard Smith J (1973) The theory of games and the evolution of animal conflict. *J Theor Biol* 47:209–221
- Milinski M (1979) An evolutionarily stable feeding strategy in sticklebacks. *Z Tierpsychol* 51:36–40
- Milinski M (1984) Competitive resource sharing: an experimental test of a learning rule for ESSs. *Anim Behav* 32:233–242
- Parker GA (1978) Searching for mates. In: Krebs JR, Davies NB (eds) *Behavioural ecology: an evolutionary approach*. Blackwell Scientific Publications, Oxford, pp 214–244
- Parker GA, Sutherland WJ (1986) Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Anim Behav* 34:1222–1242
- Power ME (1984) Habitat quality and the distribution of algae-grazing catfish in a Panamanian canal. *J Anim Ecol* 53:357–374
- Regelmann K (1984) Competitive resource sharing: a simulation model. *Anim Behav* 32:226–232
- Sargent RC, Gross MR, van den Berghe EP (1986) Male mate choice in fishes. *Anim Behav* 34:545–550
- Sutherland WJ (1982) Spatial variation in the predation of cockles by oystercatchers at Traeth Melynog, Anglesey. II. The pattern of mortality. *J Anim Ecol* 51:491–500
- Sutherland WJ (1983) Aggregation and the 'ideal free' distribution. *J Anim Ecol* 52:821–828
- Sutherland WJ, Parker GA (1985) Distribution of unequal competitors. In: Sibly RM, Smith RH (eds) *Behavioural ecology: Ecological consequences of adaptive behaviour*. Blackwell Scientific Publications, Oxford, pp 255–273
- Talbot AJ, Kramer DL (1986) Effects of food and oxygen availability on habitat selection by guppies. *Can J Zool* 64:88–93
- Zwarts L, Drent RH (1981) Prey depletion and the regulation of predator density: oystercatchers (*Haematopus ostralegus*) feeding on mussels (*Mytilus edulis*). In: Jones NV, Wolff WJ (eds) *Feeding and survival strategies of estuarine organisms*. Plenum Publishing Corp, London, pp 193–216