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Survival of the Fittest: Fish in Patchy Environments Show Ideal Free Distribution (IFD)

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Summary

Ideal free distribution (IFD) is a density-dependent model for habitat selection that predicts the distribution of mobile foragers in spatially heterogeneous (patchy) environments. The conventional IFD model assumes perfect knowledge, free transportation, and no interspecific interactions between populations of mobile foragers that distribute themselves throughout a patchy environment to maximize fitness. Habitat selection by a variety of different organisms has been observed with ideal free theory, including breeding birds, amphibians, and flying insects. The purpose of this review was to examine ideal free habitat selection in wild fish populations. Numerous studies have documented fitness equilibrium by fish in patchy environments. Furthermore, populations influenced by intraspecific competition, predator-prey dynamics, differences in competitive ability between individuals, long-term memory of habitat patches, energetic expenditure for reaching patches, and anti-predator tactics have conformed to ideal free distribution. In several cases, relaxation of the primary assumptions of free transportation and no interspecific interactions has still resulted in accurate predictions for population distribution. However, ideal free theory cannot account for populations affected by habitat confinement, nor can the model predict the distribution of organisms living in spatially homogeneous environments, or environments that are not delineated into distinct habitat patches. Furthermore, specific classes of organisms, such as parasitoids, have not been analyzed with the IFD model. Nevertheless, the support for ideal free distribution in numerous field studies, even those relaxing primary assumptions of the IFD model, suggests the notion that ideal free theory can account for fish distribution in patchy environments. Several important suggestions for future research can be drawn from the aforementioned results, including field studies to test predator and parasitoid population dynamics in response to prey distribution and conservation research to relax the primary assumption of perfect knowledge in the IFD model, ensuring the efficiency of stocking programs to preserve biodiversity in natural environments. Therefore, overall ideal free distributi[*]on has been observed in wind fish populations, providing an accurate prediction of the distribution of mobile foraging fish in spatially heterogeneous environments as well as important implications for future research.

Introduction

Environmental spatial heterogeneity, or patchiness, refers to the division of an environment into different habitat patches of varying quality that provide organisms with different levels of fitness. This has been established as a fundamental variable in the distribution of organisms (Elton 1949, 1966, Andrewartha and Birch, 1954), with different populations allocating their densities to maximize fitness within patchy environments. Ideal free distribution (IFD) is a density-dependent model for habitat selection that predicts the distribution of mobile foragers in spatially heterogeneous environments (Sutherland, 1983). Pioneered by Fretwell and Lucas (1970), the theory of ideal free habitat selection describes the equilibrium distribution of a population of competitors among two or more habitat patches of varying quality such that fitness is equalized among all individuals (Figure 1). Initially developed to account for the distribution of breeding birds, Fretwell and Lucas (1970) coined the name ideal free distribution because the studied organisms were assumed to be ideal in their judgement of profitability (Sutherland, 1983). The Fretwell and Lucas (1970) model assumes all individuals within the population are free to settle in any habitat patch, have perfect knowledge of all available patches, and do not expend time and energy to travel between patches. Furthermore, resource densities within habitat patches are held constant. An argument similar to ideal free distribution was independently proposed by Parker (1970, 1974) to describe the distribution of dungflies (*Scatophaga stercorarcia*) searching for mates. However, it is the ideal free theory developed by Fretwell and Locus (1970) that has become standard in describing habitat selection in patchy environments.

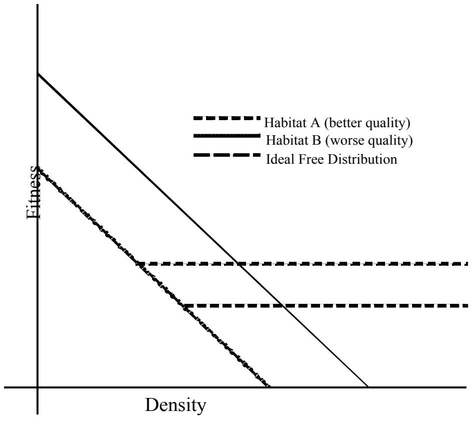

Figure 1. Conventional ideal free distribution between two habitat patches of varying quality
Fitness is equalized between populations. From Fretwell and Lucas (1970).

Ideal free distribution has been applied to the habitat selection of numerous foraging organisms, including *Bufo bufo* toads searching for mates (Davies

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and Halliday, 1979), gall aphids (*Pemphigus batae*) settling on different leaves of the narrowleaf cottonwood *Populus augustifolia* (Whittam, 1980), oystercatchers (*Haematopus ostragelus*) feeding on *Mytilus edulis* mussel beds (Zwarts and Drent, 1981), *Bombus flavifrons* bees foraging for nectar (Pyke, 1980), and mallard ducks (*Anas platyrhynchos*) feeding on bread (Harper, 1982). Ideal free theory was first applied to fish populations by Milinski (1979), who observed the equilibrium distribution of captive *Gasterosteus aculeatus* sticklebacks foraging between two habitat patches. Despite supporting IFD, the results of Milinski (1979) account only for the distribution of captive fish, not species living in natural environments. The purpose of this study therefore was to determine whether ideal free distribution has been documented in wild fish populations. Like birds and flying insects, fish are capable of moving freely between patches without being affected by habitat fragmentation, deforestation, or other problems that confine terrestrial organisms. Because the assumption of free transportation can be more easily applied to fish populations than terrestrial organisms studied with the IFD model, ideal free habitat selection can hypothetically predict the distributions of fish in spatially heterogeneous environments

Following Milinski's work, several field studies have shown that fish select habitats that maximize their fitness gain (Power, 198l, 1984; Gilliam and Fraser, 1987; Clark and Levy, 1988). Because species living in natural environments are exposed to many more variables than individuals studied under laboratory conditions, the Fretwell and Lucas (1970) model was modified in several directions to include factors such as predator-prey dynamics (Sutherland, 1983); differences in competitive ability between individuals (Sutherland and Parker, 1985; Parker and Sutherland, 1986); long-term memory of habitat patches (Milinski, 1994); energetic expenditure for reaching patches (Tyler and Gilliam, 1995); and anti-predator tactics (Rangeley and Kramer, 1998). Studies such as these help to support the notion that ideal free habitat selection can predict the distribution of fish populations in patchy environments, even when relaxing some of the primary assumptions of the Fretwell and Lucas (1970) model.

The expansion of the IFD model by Sutherland (1983) to include the variable of interspecific predator-prey interactions was the first of several changes in the Fretwell and Lucas (1970) model. Predatory fish were predicted to seek out patches of high prey density until interference with competing individuals forced them to migrate to lower density patches in order to equalize fitness. Sutherland and Parker (1985) studied individual differences that may result in ideal free habitat selection: individuals better capable of competing in high density areas were predicted to maintain their fitness while less fit individuals must seek lower density areas to achieve the same fitness. Similar studies by Parker and Sutherland (1985), Krivan (1997), and Tyler and Rose (1997) further help to explain ideal free distribution through individual variation within a population.

Milinski (1994) conducted the first study on fish long-term memory and how it affects ideal free habitat selection. In doing so, the author questioned the perfect knowledge assumption of the Fretwell and Lucas (1970) model. Although many vertebrates have been shown to retain memory of good feeding areas (Krebs, 1974; Tinbergen, 1976), Milinski questioned whether fish, particularly sticklebacks, could retain perfect knowledge of patch profitability over time in a patchy environment. Individuals were predicted to select habitats according to ideal free distribution based on previously acquired knowledge of food distribution. Tyler and Gilliam (1995) modified ideal free theory to include energetic costs in travelling between patches, creating a model called "IFD With Costs" to determine the distribution of *Rhinicthys atratulus* minnows living in fast-moving streams. Because patches upstream are more difficult and energetically costly for individuals to reach than patches downstream, the authors relaxed the primary assumption of free transportation in the IFD model and predicted that individuals would equalize their fitness based both upon competition within patches of varying quality and energetic costs required to reach these patches. IFD With Costs enabled the application of ideal free theory to environments where free transportation cannot naturally be assumed.

Rangeley and Kramer (1998) pitted ideal free distribution as an anti-predator tactic against a behavioral response to predation: aggregation. The confusion effect is a common defense against predation used by schooling fish such as juvenile pollock (*Pollachius virens*), which aggregate together to prevent predators from singling out individuals (Rangeley and Kramer, 1998). The authors suggested that environments with cover and shelter from predation would exhibit ideal free distribution among juvenile pollack, with fitness benefits gained from hiding from predators outweighing those from aggregating in open patches with more food. This study helps determine why ideal free habitat selection is more common in some environments than others.

Therefore, several studies have the potential to support the effectiveness of ideal free habitat selection in predicting the distribution of fish populations in patchy environments. Furthermore, this research suggests that the IFD model may be flexibly altered to predict distribution under a variety of environmental factors, making it ideal for the study of wild fish in spatially heterogeneous environments.

Results and Discussion

Conventional ideal free theory as a prediction of habitat selection

Fretwell and Lucas (1970) developed the theory of ideal free habitat selection to predict the distribution of breeding birds between habitat patches of different quality. Fish populations were first examined with this model by Milinski (1979), who observed fitness equilibrium by captive *Gasterosteus aculeatus* sticklebacks foraging between two habitats. Power (1984) studied armored catfish (Loricariidae) habitat selection between different pools in a Panamanian stream and observed the first significant correlation between ideal free theory and wild fish distribution. Observed pools differed from one another in sun exposure and periphyton productivity, a factor that affects food availability for the fish. Individuals distributed themselves in response to changes in the quality of pools, such that fish in sunny, crowded pools and fish in dark, sparsely-populated pools had similar rates of food intake (Figure 2; Power, 1984). Thus, the conventional IFD model created by Fretwell and Lucas (1970) adequately predicted an equalization of fitness between habitat patches of varying quality in wild populations.

An intrinsic disadvantage of ideal free theory is the assumption that all habitat patches are clearly delineated from one another. The optimal foraging theory model designed by MacArthur and Pianka (1966) predicts how an animal allocates its feeding activity in space and time. Arditi and Dacorogna (1988) modified this model and rejected the notion that environments occur in distinct patches. Animals often combine migration and foraging into one activity, feeding and traveling across habitat gradients at the same time rather than localizing themselves into distinct patches (Arditi and Dacorogna, 1988). According to the authors, species that adhere to this method of foraging cannot be studied with ideal free theory. However, Arditi and Dacorogna (1988) fail to take into account the long-term memory of animals such as antelopes grazing on the African savanna that partake in their method of optimal foraging theory (Krebs and McCleery, 1984). Although ideal free distribution cannot account for habitat selection in environments where habitat patches are not clearly delineated, Milinski (1994) identified that fish foraging across environments can remember the qualities of specific habitat patches and distribute their densities according to ideal free distribution. Thus, ideal free theory holds true for such animals when environmental spatial heterogeneity occurs.

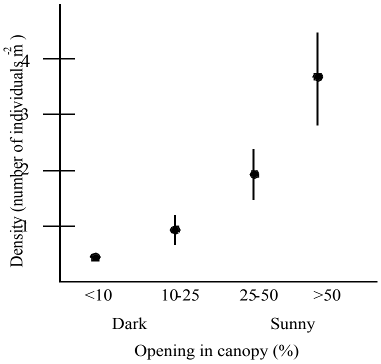

Figure 2. Armored catfish densities in pools of different canopy shading

Populations are allocated such that more individuals crowd the higher quality sunny pools than the lower quality dark pools. From Power (1984).

Long-term memory and implications for ideal free habitat selection

Milinski (1994) examined the memorization of patch profitability by individual fish when selecting between two habitats of varying quality. Three-spined sticklebacks (*Gasterosteus aculeatus*) retained the memory of patches in which they had been previously fed for eight days (Milinski, 1994). Furthermore, three days after being presented with two habitats of different food quantities, fish remembered the differences in patch quality and adjusted their densities according to ideal free theory. Individuals fed left were found in greatest abundance in the left patch, but fish fed right were also present in the left patch to minimize competition in the right patch where they were previously fed (Figure 3; Milinski, 1994). These results help to support the concept of ideal free distribution by mobile foragers. However, a drawback of Milinski's study is the assumption that individuals have free transportation to all habitat patches within an environment at any time, providing perfect knowledge and the memorization of patch profitability. Arditi and Dacorogna (1988) refute the free transportation assumption of the IFD model by providing examples of animals such as shorebirds and small mammals that are confined to particular habitat patches, either due to predation risk or habitat fragmentation. These animals do not have knowledge of better or worse habitats, and therefore cannot adjust their densities in accordance with ideal free theory. Along this line, the IFD model therefore cannot be applied to habitats fragmented due to deforestation or other methods of human intervention that confine organisms to particular areas. However, these problems are generally confined to terrestrial organisms. Although the distribution of fish can be influenced by temperature gradients and energy requirements to travel from one habitat to another, the payoff of dispersing to a habitat patch of increased quality has been shown to be a greater factor in habitat selection than confinement due to environmental factors (Tyler and Gilliam, 1995).

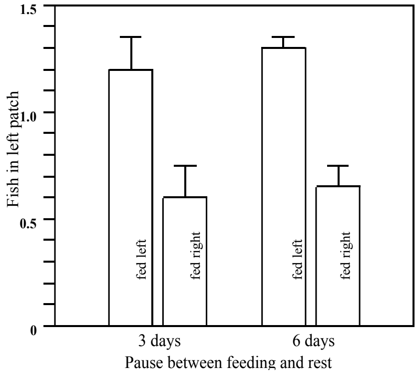

Figure 3. Distribution of sticklebacks between two habitat patches based on long-term memory

Fish were more likely to feed at the patch they previously received food from ($P<0.05$). Individuals fed right retained memory of their previous feeding location but migrated to the left patch to equalize fitness. From Milinski (1994).

Energy-expenditure and relaxing the assumption of free transportation between patches

Tyler and Gilliam (1995) observed minnow distribution in habitats of varying food quality and water velocity. IFD With Costs models were created to predict habitat selection when relaxing the assumption of free transportation between habitat patches (Figure 4). Differences in total food supply between patches were shown to induce a shift in fish distributions away from the low food patch to the high food patch when water velocities were different (Table 1). Thus, patch residence was shown to benefit fitness to a lesser extent than traveling to a habitat of greater quality, even when energy expenditure was significant (Tyler and Gilliam, 1995). These findings not only support the ideal free theory, but also suggest that stream fish integrate both energetic constraints and food acquisition in their assessment of fitness and habitat selection. Therefore, the ideal free distribution model can be flexibly altered to relax primary assumptions of habitat selection while still adequately predicting the distribution of organisms in patchy environments. Though the assumption of free transportation cannot be relaxed for terrestrial species, as stated previously, this assumption can be dropped while still maintaining ideal free distribution in aquatic populations (Tyler and Gilliam, 1995).

Predator-prey dynamics in the IFD model

Sutherland (1983) pioneered the application of predator-prey dynamics to ideal free distribution. The author relaxed the primary assumption of no interspecific interactions in the IFD model and attempted to predict predator population dynamics while foraging for prey. Predator density was allocated to habitat patches based on predator intake rate, prey density, and overall fitness as a function of interference with other predators (Sutherland, 1983). Of these three factors, only intake rate was held constant. Species with little interference were modeled to aggregate more on patches with higher prey density than on patches

Table 1. **Fish distribution between habitat patches with high and low total food**
In both slow and fast water velocity habitats fish preferred patches with greater food. From Tyler and Gilliam (1995).

	Slow water velocity		Fast water velocity	
	Low total food	High total food	Low total food	High total food
Observed (L)	1.43	2.53	3.38	4.01
Input Matching IFD/IFD With Costs I				
Prediction	2.00	2. 00	2.00	2.00
t	-2.25	0.95	2.89	4.11
P	0.074	0.387	0.034	0.009
Capture Rate Matching IFD/IFD With Costs II				
Prediction	1.87	1. 87	0.84	0.84
t	-1.76	1.18	5.33	6.49
P	0.140	0.293	0.003	0.001

with lower prey density. In contrast, species with greater interference aggregated less between habitat patches of varying fitness gain (Figure 5). Sutherland (1983) predicted an equalization of fitness within all predator populations regardless of interference level, supporting the notion that ideal free distribution can be applied to predator-prey systems. Although not tested, this model indicates the potential of ideal free theory to describe the distribution of predators in patchy environments.

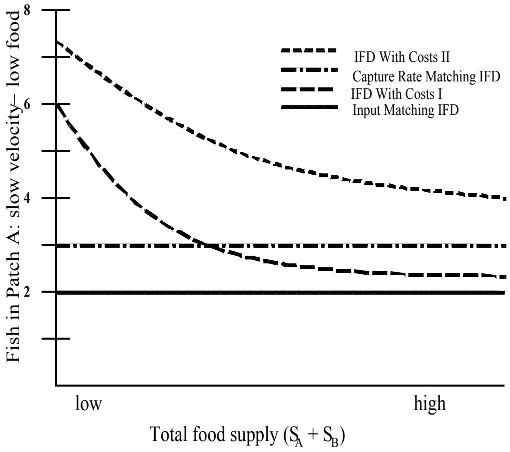

Figure 4. Predicted fish distribution for IFD With Costs models
Population density in the low velocity water patch decreases as food supply increases. From Tyler and Gilliam (1995).

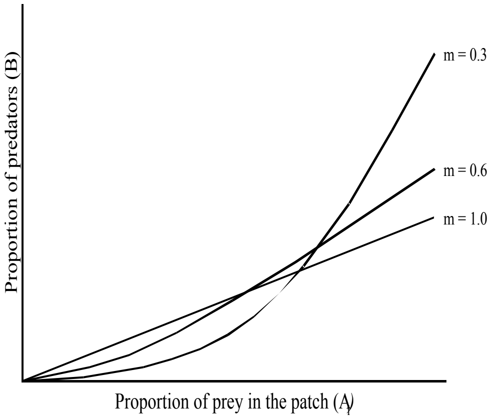

Figure 5. Aggregative numerical response for different levels of predator interference (m)
Increased prey density results in greater interference for competing predators. From Sutherland (1983).

While the findings of Sutherland (1983) can hypothetically account for the habitat selection of predators, information on ideal free distribution by parasitoids, a particular subcategory of predatory organisms that lay eggs on hosts to kill them, is inherently lacking in the field. Evidence currently exists to suggest that parasitoid distribution is influenced both by prey dispersion to different habitats (Waage, 1979; Hassell, 1980) and interference (Hassell, 1978), though these concepts have never been applied to the IFD model. Thus, field evidence to support the prediction of predator and parasitoid distribution in patchy environments is significantly lacking. However, ideal free distribution has been observed in prey populations threatened by predation (Rangeley and Kramer, 1988). Although ideal free theory has not been applied to predator habitat selection as a result of prey distribution, the population dynamics of prey in predator-prey environments has been accounted for by the IFD model.

Anti-predator tactics and ideal free distribution

Rangeley and Kramer (1998) applied ideal free theory to the habitat selection of prey in a high predation environment. Juvenille pollock (*Pollachius virens*) distributed themselves to maximize fitness – measured as survival probability – by crowding under algal mats to hide from avian predators, such as the cormorant (*Phalacrocoras auritus*) (Figure 6). Fish aggregated more in open habitats devoid of shelter from avian predators, and aggregated less when under the cover of algae, suggesting use of the confusion effect when exposed to predators (Rangeley and Kramer, 1998). These results show that fish distributed themselves to

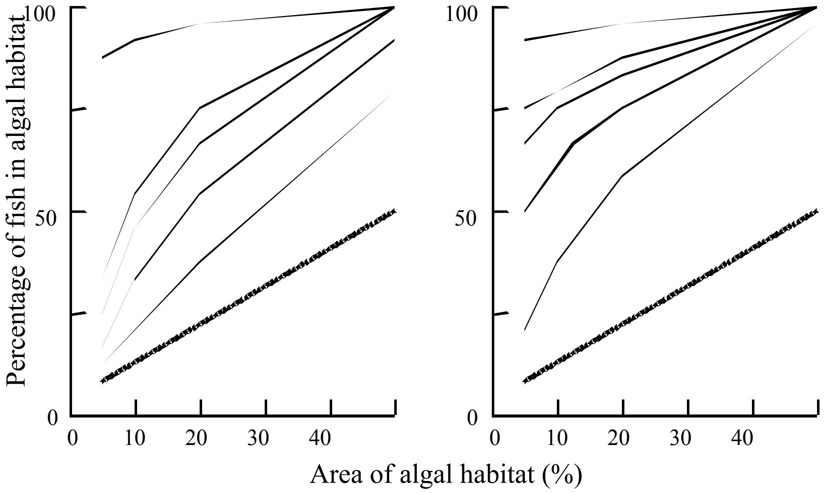

Figure. 6. Distribution of juvenille pollack in algal habitat patches before and after predation
Fish maximized fitness by seeking shelter from predators. From Rangeley and Kramer (1998).

maximize, with most individuals distributed underneath the algae and the remaining fish migrating to the open patches, where they aggregated to deter predatory birds. As such, the findings of Rangeley and Kramer (1998) suggest that the IFD model is capable of taking into account multiple factors that influence fitness. In this case, shelter from predators and food acquisition were observed as key factors influencing the habitat selection of juvenille pollock. Thus, overall ideal free distribution accurately predicted the habitat selection of fish despite relaxing the primary assumption of no interspecific interactions, supporting the application of the IFD model to fish in spatially heterogeneous habits.

Conclusion

Ideal free distribution has been observed in wild fish populations influenced by intraspecific competition (Power, 1984), long-term memory of habitat patches (Milinski, 1994), energetic constraints between patches (Tyler and Gilliam, 1995), predator-prey dynamics (Sutherland, 1983), differences in competitive ability between individuals (Sutherland and Parker, 1985; Parker and Sutherland, 1986), and anti-predator tactics (Rangeley and Kramer, 1998). Initially observed by Milinski (1979) in captive sticklebacks, ideal free distribution has proven an effective model in predicting the distribution of fish in spatially heterogeneous habitats, even when relaxing the primary assumptions of the Fretwell and Lucas (1970) model. The results of these studies present several possibilities for future research. First, a field test for the Sutherland (1983) model would validate whether or not ideal free distribution can accurately predict the population dynamics of predators foraging for prey. Although other studies have emphasized prey response to predator distribution in the IFD model (Rangeley and Kramer,1998), predator habitat selection has not been observed in patchy environments.

The Sutherland (1983) model also presents a useful platform for studying parasitoid population dynamics, specifically the distribution of aquatic parasitoids such as the hagfish. Because parasitoid habitat selection has been correlated to prey distribution and interference, two variables accounted for by Sutherland (1983), the model has realistic potential to not only explain the population dynamics of predators but parasitoids as well. Finally, future ideal free theory research should focus on relaxing the assumption of perfect knowledge in fish introduced to environments with no previous knowledge of patch profitability. This path of fieldwork has significant implications for conservation projects, as fish raised in hatcheries have no knowledge of habitat patch quality when introduced to new environments. Stocking projects are an important aspect of maintaining healthy wild populations, especially in areas subjected to fishing pressure. Therefore, research emphasizing the acquisition of knowledge about patch profitability by fish in an unknown habitat and whether or not this leads to fitness equalization and ultimately survival is of the utmost importance. This knowledge, in turn, will maximize stocking efficiency in conservation programs trying to preserve fish biodiversity in many environments. Thus, overall the ideal free habitat selection model pioneered by Fretwell and Lucas (1970) has been applied to fish in spatially heterogeneous environments under a variety of conditions. The IFD model has been modified in several directions to account for the many variables of the natural world, and as a result of this research several important future projects, including the conservation of stocked fish populations, have been suggested.

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