International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

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Foraging on spatially distributed resources with sub-optimal movement, imperfect information, and travelling costs: Departures from the ideal free distribution

Shuichi Matsumura (matsumur@gifu-u.ac.jp)
Robert Arlinghaus (arlinghaus@igb-berlin.de)
Ulf Dieckmann (dieckmann@iiasa.ac.at)

Approved by

Detlof Von Winterfeldt
Director

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Title

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Authors' names and addresses

Shuichi Matsumura[1,2], Robert Arlinghaus[2,3], and Ulf Dieckmann[1]

[1] Evolution and Ecology Program, International Institute for Applied Systems Analysis, Schlossplatz 1, 2361 Laxenburg, Austria

[2] Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany

[3] Inland Fisheries Management Laboratory, Department for Crop and Animal Sciences, Faculty of Agriculture and Horticulture, Humboldt-University of Berlin, Philippstrasse 13, Haus 7, 10115 Berlin, Germany

Corresponding author

Shuichi Matsumura
Faculty of Applied Biological Sciences, Gifu University, Yanagido 1-1, Gifu City, 501-1193 Gifu, Japan
phone: +81-58-2932874, fax +81-58-293-2840, email: matsumur@gifu-u.ac.jp

Abstract

Ideal free distribution (IFD) theory offers an important baseline for predicting the distribution of foragers across resource patches. Yet it is well known that IFD theory relies on several over-simplifying assumptions that are unlikely to be met in reality. Here we relax three of the most critical assumptions: (i) optimal foraging moves among patches, (ii) omniscience about the utility of resource patches, and (iii) cost-free travelling between patches. Based on these generalizations, we investigate the distributions of a constant number of foragers in models with explicit resource dynamics of logistic type. We find that, first, when foragers do not always move to the patch offering maximum intake rate (optimal foraging), but instead move probabilistically according to differences in resource intake rates between patches (sub-optimal foraging), the distribution of foragers becomes less skewed than the IFD, so that high-quality patches attract fewer foragers. Second, this homogenization is strengthened when foragers have less than perfect knowledge about the utility of resource patches. Third, and perhaps most surprisingly, the introduction of travelling costs causes departures in the opposite direction: the distribution of sub-optimal foragers approaches the IFD as travelling costs increase. We demonstrate that these three findings are robust when considering patches that differ in the resource's carrying capacity or intrinsic growth rate, and when considering simple two-patch and more complex multiple-patch models. By overcoming three major over-simplifications of IFD theory, our analyses contribute to the systematic investigation of ecological factors influencing the spatial distribution of foragers, and thus help in deriving new hypotheses that are testable in empirical systems. A confluence of theoretical and empirical studies that go beyond classical IFD theory is essential for improving insights into how animal distributions across resource patches are determined in nature.

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Understanding the distribution of animals among spatially structured resources is one of the most important subjects in basic and applied ecology. Analogous questions apply to human predators such as hunters, commercial fishers, and recreational anglers. In this context, the ideal free distribution (IFD) theory, originally developed by Fretwell and Lucas (1970) to predict habitat selection by birds, keeps attracting considerable attention in terms of theoretical investigations and applications to a wide range of species (e.g., Tregenza 1995, Gillis 2003, Křivan et al. 2008, Houston 2008). Its predictions have been tested in detailed experiments, mainly using fish (e.g., Milinski 1979, 1984, Kennedy et al. 1994, Hakoyama and Iguchi 2001) or birds (e.g., Harper 1982, Inman 1990, Kennedy and Gray 1997, Vahl et al. 2007), as well as in large-scale field studies (e.g., Gillis 2003, Haugen et al. 2006, Jones et al. 2006). Although the original IFD model was successful in predicting the distribution of foraging animals, a characteristic bias has been reported in empirical studies since the early stages of application (Abrahams 1986): resource patches of poorer quality generally attract more foragers than predicted by classical IFD theory, while patches of better quality attract fewer foragers (summarised by Kennedy and Gray 1993). This deviation from theoretical predictions has stimulated critical examination and subsequent extension of the original IFD model.

Classical IFD theory relies on several simplifying assumptions that are unlikely to be met in the real world. In an extensive review of IFD studies, Tregenza (1995) classified such assumptions into the following seven categories: (1) equal competitive abilities among foragers, (2) omniscience of foragers, (3) cost-free travelling of foragers between patches, (4) no interference competition among foragers, (5) fixed resources in space and time, (6) rate of resource intake as the only factor affecting the patch choice of foragers, and (7) distribution of foragers determined entirely by maximizing their short-term fitness. It is therefore not surprising that scholars have tried to relax some of these simplifying assumptions to better understand the spatial distribution of foragers. However, not all aspects and variables summarized in this list have been investigated in detail as regards their influence on the distribution of foraging animals. Tregenza (1995) pointed out that a vast majority of the efforts to extend the original IFD model had been devoted towards analysing competition among foragers (assumptions 1 and 4), sometimes in conjunction with modifications of resource dynamics (assumption 5). This trend has continued until today (Tregenza et al. 1996, van der Meer 1997, van der Meer and Ens 1997, Weber 1998, Doncaster 1999, 2000, Ollason and Yearsley 2001, Flaxman and Reeve 2006, Smallegange and van der Meer 2009).

Despite their importance, substantially less attention has been devoted to critically examining the impact of the other simplifying assumptions. Investigating how relaxing these other assumptions of the original IFD theory changes common predictions about the distribution of foragers among spatially structured resources is needed before more realistic predictions, applicable to empirical systems, can be obtained. It is therefore desirable to conduct a systematic investigation in which more than one assumption is relaxed simultaneously. Unfortunately, this has rarely been attempted in the literature. To fill this gap, the research presented in this study relaxes three critical assumptions of the original IFD model – (i) optimal foraging moves among patches, (ii) omniscience about the utility of resource patches, and (iii) cost-free travelling between patches – and examines in a general and systematic way the impacts of the relaxed assumptions on departures from IFD predictions. Only by incorporating these relaxations into a common model, the individual and joint contribution of these assumptions on forager distributions can be comprehensively explored.

The original IFD model assumes that at each foraging animal always chooses the patch providing it with the highest utility in terms of resource intake rate. Clearly, this strict assumption of optimal foraging is not satisfied in nature. Thus, several authors have incorporated non-optimal, probabilistic movement into their models (Regelmann 1984, Houston and McNamara 1987, Hugie and Grand 2003, Ruston and Humphries 2003, Jackson et al. 2004) and found that forager distribution then become more uniform (with poor patches attracting more foragers) than predicted by classical IFD theory. Unfortunately, these investigations were limited to simple situations with two resource patches, and thus omitted multi-patch scenarios. Moreover, they considered rigid, and probably unrealistic, assumptions about a fixed mixture of fully optimal and fully random foraging movements, with this mixture remaining unaffected by actual differences in utility between resource patches. More realistic sub-optimal foraging movement has been investigated only for the special case in which foragers move optimally, unless the difference of two patch utilities is smaller than a given threshold, whereupon they more randomly (perceptual-constraints models). These studies predicted that the forager distribution becomes less skewed than the IFD (Abrahams 1986, Kennedy and Gray 1993, Spencer et al. 1995, 1996, Carter and Abrahams 1997, Collins et al. 2002). However, instead of assuming that the nature of foraging movements changes abruptly below a threshold, it is more natural to assume that the degree of sub-optimality in foraging movement due to errors in patch choice increases gradually as utility differences between patches decrease (Egas et al. 2004). In the present study, we therefore adopt a gradual and probabilistic approach to patch choice, in an effort to complement the existing literature and to test the generality of the aforementioned findings.

It is also obvious that real foragers are never omniscient, in the sense that they would possess perfect information about expected intake rates in spatially segregated resource patches. Some models have therefore dealt with situations in which foragers have imperfect information about the utility of resource patches, and need to improve their knowledge through experience (Bernstein et al. 1988, 1991, 1999, Cézilly and Boy 1991, Koops and Abrahams 2003, Hakoyama 2003, Cressman and Křivan 2006). These models were typically individual-based, and incorporated imperfect information together with many other realistic assumptions. As a result, they provided no clear answer to the question what kinds of departures from the IFD were attributable to the assumption of imperfect information, as opposed to relaxations of other simplifying assumptions. As a remarkable exception, Ranta et al. (1999, 2000) reported that the distribution of foragers across resource patches becomes less skewed than the IFD in simple but insightfully constructed cellular-automaton models in which the knowledge of foragers was limited to a certain range around their current locations. However, instead of assuming an abrupt absence of information beyond a certain distance, it is again more natural to assume that the reliability of information foragers have on patch utilities decreases continuously as the distance to their current patch increases. Our model therefore incorporates a gradual decline in foragers' knowledge of patch utility with distance – an assumption that, to our knowledge, has as yet not been used for extending the original IFD model.

Finally, the impact of cost of travelling between patches on departures from IFD-based predictions has attracted even less research than the effects of sub-optimal movement and imperfect information. Some researchers introduced travelling costs in terms of foraging time in individual-based simulation models (Regelman 1984, Bernstein et al. 1991, Cézilly and Boy 1991), and reported a decrease in the frequency of patch switching (Regelman 1984). Although Bernstein et al. (1991) established that the resultant distribution of foragers departed from the IFD, they did not explain these departures in detail. Using analytical models, both Kennedy and Gray (1993) and Morris (1987) predicted that with increasing travel costs the distribution of foragers among spatially structured resources becomes more extreme relative to the IFD (with richer patches attracting more foragers). However, the model by Kennedy and Gray (1993) was criticised, mainly because they extended a model based on individual behaviours to a group (Milinski 1994, Åström 1994, Lessells 1995). Also, conclusions reported by Morris (1987) were based on the assumption of unidirectional migration from a richer habitat to a poorer one; a simple extension of his model by Åström (1994) later showed that effects of travelling costs on bidirectional movements could potentially cancel out. Åström (1994) thus predicted that travelling cost would not have any consistent impact on forager distributions across patches. Being aware of possible confounding factors, Åström (1994) concluded that more detailed, mechanically based models were needed to understand in greater detail the effects of travelling costs on distributions of foragers. Unfortunately, however, no study appears to have responded to his call – an observation that, in part, motivated the present study.

In conclusion, the scope of existing investigations on the effect of sub-optimal foraging movement, imperfect information, and travelling costs on distributions of foragers across spatially structured resource patches is quite limited, and no study so far has investigated interactions among these aspects. This state of affairs prevents researchers from fully understanding factors affecting forager distributions in nature and burdens the application of IFD theory to empirical systems with considerable uncertainties. The objective of the present study is to relax the assumptions of (i) optimal foraging moves among patches, (ii) omniscience about the utility of resource patches, and (iii) cost-free travelling between patches, by systematically investigating their separate and joint impact on the distribution of foragers across resource patches. We also incorporate and systematically evaluate other features that might be important in natural systems, such as variability across patches in the carrying capacities and intrinsic growth rates of resource populations. To further assess the generality of our findings, we present results for two general models, describing a two-patch system and a multi-patch system, respectively. We start with analyzing two-patch systems, thereby following a common approach in previous IFD studies (e.g., Milinski 1979, Parker and Sutherland 1986), before we proceed to more general models with multiple patches. We introduce sub-optimal movement decreasing with the utility difference between resource patches, and study information uncertainty increasing with the distance between resource patches. In this manner, we are able to confirm and extend conclusions previously reached by studies that were based on more restrictive assumptions. We also report a surprising new finding, that distributions of sub-optimal foragers approach the IFD as travelling costs are raised.

Model description

In this study, we systematically relax three of the critical assumptions of the original IFD model: (i) optimal foraging moves among patches, (ii) omniscience about the utility of resource patches, and (iii) cost-free travelling between patches (Fig. 1).

Spatial structure among patches

In our model, a constant number of foragers (which might be predators or parasites) move among resource patches. The resource (which serves as prey for the predators, or as host for the parasites) does not move among patches, but its abundance in each patch changes according to population dynamics with logistic growth and exploitation. This situation is characteristic of systems in which the resource has a comparatively high rate of renewal compared to changes in the abundance of foragers. Typical examples include birds feeding on a metapopulation of insects or fish, or fishers targeting spatially distributed fish stocks across a network of lakes or marine fishing grounds.

We investigate two types of spatial structures: two-patch and multi-patch models. In the two-patch model, only two resource patches are considered, which differ from each other either in their carrying capacity K or in their intrinsic growth rate r. We first consider this simple situation because two-patch systems have been used in most experimental studies (e.g., Milinski 1979, 1984) and corresponding theoretical investigations (Regelman 1984, Parker and Sutherland 1986). In the multi-patch model, a two-dimensional square lattice of $10 \times 10 = 100$ patches is considered. To remove edge effects, we use periodic boundary conditions (so that the right edge of the lattice is connected to the left edge, and the top edge is connected to the bottom edge, resulting in a torus-like structure; e.g., Adler and Nuernberger 1994). Similar to the two-patch model, patches differ either in their carrying capacities or intrinsic growth rates, following normal distributions around a given mean (mean of K = 600 with s.d. of K = 100, or mean of r = 0.3 with s.d. of r = 0.05). The spatial distribution of patches is initially assumed to be independent of their quality, i.e., there is no correlation between the qualities of neighbouring patches.

We examine the distribution of foragers and the corresponding resource abundances at equilibrium. Equilibrium distributions of foragers and abundances of the resource are determined either by numerically solving the underlying equations or by conducting numerically simulations in discrete time. We treat both the number of foragers across patches and the resource abundances within patches as continuous variables. The system is deemed to have reached equilibrium when the relative changes between consecutive time steps of resource abundances in all patches fall below a fixed threshold (0.001). We define the IFD as the distribution of foragers that causes the intake rates of resource at equilibrium to be identical across all resource patches.

Resource dynamics within patches

We consider a renewable resource that is regulated by logistic growth and exploitation, resulting in a widely used kind of resource dynamics in discrete time (e.g., Clark 1990, Vandeermeer and Goldberg 2003). Specifically, the resource dynamics of the i th patch is described by

$$R_i(t+1) = R_i(t)\exp\{r_i(1 - R_i(t)/K_i) - qF_i(t)\},$$

where K_i is the patch's carrying capacity, r_i is its intrinsic growth rate, F_i is the number of foragers currently occupying the patch, and q is their foraging rate. We assume that density-dependent resource renewal and foraging occur sequentially. With $R_i(t)$ representing the resource abundance after renewal, the amount of resource consumed at time t is

$$C_i(t) = R_i(t)\{1 - \exp(-qF(t)_i)\}.$$

Because $r_i(1 - R(t)_i / K_i) - qF_i(t) = 0$ at equilibrium, the resource abundance and the number of foragers at equilibrium, R_i^* and F_i^*, are related by

$$R_i^* = K_i(1 - qF_i^* / r_i).$$

The equilibrium intake rate V_i^* is the amount of resource consumed per forager per time step,

$$V_i^* = C_i^* / F_i^* = R_i^*\{1 - \exp(-qF_i^*)\} / F_i^* = K_i(1 - qF_i^* / r_i)\{1 - \exp(-qF_i^*)\} / F_i^*.$$

If the distribution of foragers follows the IFD, foragers in any patch by definition experience identical intake rates. We therefore calculate the number of foragers F_i^* for $i = 1, \ldots, n$ under IFD conditions by numerically solving the equations

$$K_1(1 - qF_1^* / r_1)\{1 - \exp(-qF_1^*)\} / F_1^* = K_2(1 - qF_2^* / r_2)\{1 - \exp(-qF_2^*)\} / F_2^* = \ldots,$$

with

$$F_{\text{tot}} = \sum\nolimits_{i=1}^{n} F_i^* ,$$

denoting the total number of foragers in the system, which is assumed to be constant.

Forager movement between patches

Foragers are assumed to move between patches probabilistically according to the utility that is provided by a given patch. The probability of moving from patch i to patch j is defined as

$$M_{ij} = \exp(\alpha U_{ij}) / \sum\nolimits_{k=1}^{n} \exp(\alpha U_{ik}) ,$$

where U_{ij} denotes the utility of patch j from the perspective of individuals in patch i, and α is an parameter controlling the degree of optimality in the movement of foragers. The basic assumption underlying this equation is that foragers are likely to make errors in acting upon their knowledge about the utilities of patches, preventing them from always moving optimally as the IFD model assumes. Such errors are more pronounced when foragers experience smaller utility differences between patches (Egas et al. 2004). Accordingly, in our model, foragers move exclusively to the patch with the highest utility value when $\alpha \to \infty$, while they move randomly when $\alpha = 0$. In other words, the movement of foragers agrees with the IFD assumption when $\alpha \to \infty$, while a decrease in α causes an increase in the degree of non-IFD or sub-optimal movement (Fig. 1 a).

When incorporating imperfect information about the utility of patches and costs for travelling between patches, the perceived utility of patch j for foragers in patch i is defined as

$$U_{ij} = \left\{ I_{ij} V_j + (1 - I_{ij}) \bar{V}_i \right\} - T_{ij} ,$$

where V_j is the utility of patch j and T_{ij} is the cost of travelling from patch i to patch j. I_{ij} denotes the certainty of information foragers in patch i have about patch j ($0 \le I_{ij} \le 1$). By weighting the utility of other patches k with the degree of information certainty a forager in patch i has about these utilities,

$$\bar{V}_i = \frac{\sum_{k=1}^{n} I_{ik} V_k}{\sum_{k=1}^{n} I_{ik}},$$

we obtain the average utility among patches as perceived by foragers in patch i. Therefore, the expected utility U_{ij} of patch j as perceived from patch i is the utility V_j of patch j when foragers have perfect information about that patch ($I_{ij} = 1$), while U_{ij} approaches the average $\bar{V}_i$ as the information certainty vanishes ($I_{ij} \to 0$). In other words, foragers replace missing information by average information. In the present study, the utility V_j of a patch j is given by the resource intake rate of foragers in that patch (this is motivated by the often close relation between the intake of resources and the survival and/or reproduction of foragers).

Travelling costs and uncertainty about patch utility are assumed to increase with the distance between patches. The distance between any two neighbouring patches i and j is assumed to be $d_{ij} = 1$. This implies that the maximum distance between patches in a two-dimensional lattice within 10×10 patches is $5\sqrt{2}$. Geometric decay with distance is assumed for the certainty of information about patch utility,

$$I_{ij} = I_1^{d_{ij}},$$

where I_1 is the information certainty when the inter-patch distance is 1 (Fig. 1 b). We assume that travel costs increase linearly with inter-patch distance,

$$T_{ij} = T_1 d_{ij},$$

where T_1 is the travelling cost when the inter-patch distance is 1 (Fig. 1 c). In the present study, we assume that travelling costs and information certainties are symmetric within pairs of patches ($I_{ij} = I_{ji}$ and $T_{ij} = T_{ji}$). In the analyses below, we vary information uncertainty $\phi_1 = 1 - I_1$ ($0 \le \phi_1 \le 1$), so that the IFD conditions are described by $\phi_1 = T_1 = 0$ and $\alpha \to \infty$.

Outline of analysis

Figure 1 summarises the scheme of our systematic investigation of effects of relaxing three simplifying assumptions of classical IFD theory – by considering sub-optimal foraging, information uncertainty, and travelling costs – on the equilibrium distribution of foragers among resource patches. We start with investigating the two-patch model. Our analyses unfold as follows:

- In a first step, we examine the baseline situation in which foragers experience no travelling costs and have perfect information about intake rates across all patches. We then alter the optimality of foraging movements and compare non-IFD ($\alpha < \infty$) with IFD ($\alpha \to \infty$) situations.
- In a second step, we introduce information uncertainty about patch utility. We compare the resultant distribution of foragers with IFD predictions.
- In the third step, we add travelling costs between patches and again contrast the resultant distribution of foragers with IFD predictions.

Finally, we repeat the above three steps for the multi-patch model.

In each step, the equilibrium distribution of foragers and the corresponding intake rates in each resource patch are calculated by discrete-time simulations. When the system has reached equilibrium, we record the number of foragers and the intake rates in each resource patch. Additionally, we obtain the IFD for $\alpha \to \infty$ and $\phi_1 = T_1 = 0$ by solving equations numerically, as described above.

The generality of our results is tested by modifying the total number of foragers in the system, as well as by changing the nature and degree of heterogeneity in patch quality through variations in the distribution of carrying capacities and intrinsic growth rates of the resource across patches.

Results

Two-patch model

In the two-patch model, we assume that there are only two patches, with one patch P having poorer resource quality, in terms of either carrying capacity K or intrinsic growth rate r, than another patch R.

We start by examining the baseline case in which foragers experience no travelling costs between the two patches ($T_{\mathrm{PR}} = 0$), and have perfect information about the two patch utilities ($\phi_{\mathrm{PR}} = 0$), even though they do not necessarily move between patches optimally ($\alpha < \infty$). At equilibrium and with optimal movement ($\alpha \to \infty$), the poor patch P hosts fewer foragers than the rich patch R, $F_{\mathrm{P}}^{*} < F_{\mathrm{R}}^{*}$ (Fig. 2 a, b). The equilibrium proportion of foragers in the poor patch, $F_{\mathrm{P}}^{*} / (F_{\mathrm{P}}^{*} + F_{\mathrm{R}}^{*})$, increases as the movement optimality α is reduced, i.e., as movement patterns depart more and more from being optimal (Fig. 2 a, b). In other words, the distribution of foragers is less skewed between the two patches of different resource qualities when foragers choose patches sub-optimally and probabilistically ($\alpha < \infty$), than when they do so optimally and deterministically ($\alpha \to \infty$)

as assumed by classical IFD theory. By definition, there is no difference in the intake rates of the two resource patches under IFD conditions. Under sub-optimal movement, the intake rate in the rich patch is always higher than in the poor patch, but this disparity decreases as the movement optimality α increases (Fig. 2 c, d). We observe qualitatively similar patterns when the two resource patches differ in either carrying capacity K (Fig. 2 left) or intrinsic growth rate r (Fig. 2 right).

Next, we investigate the impact of forager number and of the magnitude of inter-patch difference in resource quality on the distribution and intake rates of foragers under the baseline condition of no travelling cost and perfect information. If foragers move sub-optimally ($\alpha < \infty$), their equilibrium proportions approach the IFD when the total number of foragers in the system increases (Fig.3 a, b) and when the difference in patch quality decreases (Fig.3 c, d). It is interesting to observe that when the assumptions of the original IFD model are satisfied (i.e., $\alpha \to \infty$), the poor patch may host no foragers at all when the total number of foragers is small (Fig. 3 a) or when its carrying capacity is much smaller than that of the rich patch (Fig. 3 c). This situation does not qualitatively change when forager movement is close to optimal ($\alpha = 5$). As the optimality of forager movement between patches declines ($\alpha = 1$), the poor patch always attracts some foragers. Sub-optimal movement tends to result in a greater disparity in average intake rates between the poor and the rich patch. In general, this disparity in intake rates decreases as the forager distribution approaches the IFD, i.e., as the number of foragers increases and the inter-patch difference in resource qualities decreases (Fig. 3 e-h). Interestingly, this effect is less pronounced when resource patches differ in intrinsic growth rate (Fig. 3 f, h) than when they differ in carrying capacity (Fig. 3 e, g).

The introduction of information uncertainty has a systematic impact on the forager distribution. Under the baseline condition of perfect information ($\phi_1 = 0$) with sub-optimal movement ($\alpha < \infty$), the forager distribution is less skewed than the IFD (Fig. 4 a). As information uncertainty increases, the forager distribution becomes even less skewed and approaches an even distribution of foragers across the rich and poor patches, resulting in equilibrium proportions of 0.5 in both patches (Fig. 4 a). The disparity in intake rates rises as information uncertainty is aggravated (Fig. 4 d). We observe the same trends independent of whether the two patches differ in carrying capacities or intrinsic growth rates (results not shown). The effects of information uncertainty disappear when foragers choose their patches optimally ($\alpha \to \infty$): even though differences in perceived patch utilities diminish as uncertainty increases, optimal foragers are assumed to be able to recognise even the most minute differences in patch utilities, so that they can always choose the best patch.

Compared with information uncertainty, travelling costs have the opposite effect on the distribution of foragers (Fig. 4 b). Under the baseline condition of no travelling costs ($T_1 = 0$) with sub-optimal movement ($\alpha < \infty$), the forager distribution is less skewed than the IFD. As travelling costs increase, the proportion of foragers in the poor patch decreases and thus approaches the IFD (Fig. 4 b). The same effect occurs when foraging movement becomes closer to being optimal, i.e., when α increases. As departures from the IFD diminish, the disparity in intake rates between the patches decreases (Fig. 4 e). We observe the same trends independent of whether the two patches differ in carrying capacities or intrinsic growth rates (results not shown). The effects of travelling costs disappear when foragers always choose the best patch, i.e., when they move optimally ($\alpha \to \infty$). In that extreme case, the unique equilibrium of proportions in each patch is replaced with an equilibrium range that changes with travelling costs (shaded area in Fig. 4 b). The equilibrium range spreads symmetrically on both sides of the IFD and becomes wider when travelling costs are increased. Within this range, the intake rate in one patch may be slightly higher than in the other, but the travelling costs cancel out any potential benefit, thereby effectively preventing forager movement.

Finally, we examine the case in which travelling costs and imperfect information apply together. The results show that in their effects on the forager distribution these two factors always act antagonistically, i.e., they diminish each other's effects (Fig. 4 c; only the case $\alpha = 1$ is shown).

Multi-patch model

In the multi-patch model, we consider a square lattice of $10 \times 10 = 100$ patches, which differ from each other in either their carrying capacity K or intrinsic growth rate r.

We start by investigating the impact of sub-optimal movement when K varies among patches. In the IFD model, foragers move among patches until they can no longer increase their intake rate: as a result, some low-quality patches host no foragers, in particular when the total number of foragers is low (Fig. 5 a, dotted IFD lines). Accordingly, the IFD becomes more uniform as the total number of foragers increases. When we introduce sub-optimal foraging movement ($\alpha < \infty$), the forager distribution becomes less skewed than the IFD (Fig. 5 a). The difference in intake rates among patches increases as movement optimality declines (Fig. 5 c).

The forager distribution behaves differently when the intrinsic growth rate r rather than the carrying capacity K varies between patches (Fig. 5 b). The IFD is then characterized by linear relationships between a patch's intrinsic growth rate and its number of foragers, and even the lowest-quality patches always attract some foragers. An analytical investigation of this pattern is provided in the Appendix. The forager distribution does not become more uniform when the total number of foragers increases. Despite these differences in the IFDs resulting from variability among patches in K or r, the effect of movement optimality is similar in both cases: as movements depart more from being optimal, the forager distribution becomes less skewed than the IFD and the disparity of intake rates among patches increases (Fig. 5 d).

As in the two-patch model, information uncertainty has systematic effects on the forager distribution. The baseline distribution under perfect information ($\phi_1 = 0$) and sub-optimal movement ($\alpha < \infty$) is less skewed than the IFD, and information uncertainty causes the forager distribution to become even more uniform across patches (Fig. 6 a), which increases the disparity of intake rates among patches (Fig. 6 d). Imperfect information has the same consistent effects on the forager distribution independent of whether the variation among patches occurs in carrying capacity K or intrinsic growth rate r (results not shown). Depending on the quality of its neighbouring patches, a patch of given quality hosts slightly different numbers of foragers at equilibrium: low-quality patches host more foragers when they are surrounded by high-quality patches than when they are surrounded by low-quality patches, because in the former case the surrounding source population is larger. This effect does not occur when information and travelling costs are independent of the distance between patches.

Travelling costs bias forager distributions and disparities of intake rates among patches in the opposite direction than information uncertainty. The baseline forager distribution under cost-free travel ($T_1 = 0$) and sub-optimal movement ($\alpha < \infty$) is less skewed than the IFD (Fig. 6 b). As travelling between patches becomes more costly, the forager distribution becomes more skewed and approaches the IFD (Fig. 6 b). Accordingly, the disparity of intake rates among patches diminishes as travelling costs increase (Fig. 6 d). We observe the same trends for variability among patches in K and r (results not shown). Analogous to the case of information uncertainty, the equilibrium number of foragers a patch of certain quality attracts under travelling costs depends on the quality of its neighbouring patches.

The consistent effects resulting from information uncertainty and travelling costs are observed only when foragers respond sub-optimally to the intake rates available across patches ($\alpha < \infty$). For optimal movement ($\alpha \to \infty$), neither information uncertainty nor travelling costs change the forager distribution. Instead, we find equilibrium ranges of forager numbers in each patch, as in the two-patch case.

Finally, we examine the case in which information uncertainty and travelling costs are varied jointly. In these cases, the forager distribution is always less skewed than the IFD. Departures from the IFD grow as information certainty and travelling costs decrease, with the two factors here acting synergistically (Fig. 6 c; only the case $\alpha = 1$ is shown).

One may wonder whether the impact of travelling costs on forager distributions depends on the assumed absence of correlations between the resource qualities of neighbouring patches. In natural systems, the resource qualities of adjacent patches are likely to be similar. We therefore vary the degree of spatial autocorrelation in the resource qualities of neighbouring patches and check how this affects the forager distribution. We find that the forager distribution departs less from the IFD when positive correlations reinforce the impact of travelling costs (Fig. 7).

Overall, the results of the multi-patch models are in good agreement with the results of the two-patch model. Sub-optimal movement results in less skewed forager distributions among patches, and the introduction of information uncertainty enhances these departures from the IFD. Interestingly, travelling costs have the opposite effect, with forager distributions approaching the IFD as travelling costs increase.

Discussion

Using a theoretical modelling approach, here we have investigated the distribution of foragers across multiple resource patches under more realistic conditions than those assumed by the original IFD model (Fretwell and Lucas 1970). Specifically, using general two-patch and multi-patch models with resource renewal and constant forager numbers, we analysed the impacts of sub-optimal foraging moves among patches, of information uncertainty about patch utility, and of costs of travelling between patches. We found that when non-ideal foragers probabilistically move between patches according to the resource intake rates available among patches, their distribution is less skewed than the IFD, so that low-quality patches attract more foragers than expected under IFD conditions. We also found that the forager distribution becomes more uniform across patches when foragers do not possess perfect information about patch utilities. To our surprise, the introduction of costs of travelling between patches had an impact in the opposite direction, rendering the forager distribution across resource patches more similar to IFD predictions. The effects of the three investigated factors appear to be robust: we found equivalent effects when examining a two-patch and a multi-patch model, when considering variability in the carrying capacity K or the intrinsic growth rate r of patches, and when changing the spatial autocorrelation of patch qualities among neighbouring patches.

Our study is the first joint and systematic investigation of the impact of sub-optimal foraging movement, information uncertainty, and travelling costs in a general model predicting the distribution of foragers. Our results considerably extend the existing theoretical literature on IFD theory and its limitations, provide mechanistic explanations of forager distributions observed in nature, and are useful for deriving hypotheses about, and predictions of, forager distributions in specific ecological systems.

The first key assumption of our model that differs from previous IFD models is that foragers respond probabilistically to differences in patch utility. In other words, we not only incorporate non-IFD, sub-optimal movement among patches (Regelmann 1984, Houston and McNamara 1987, Hugie and Grand 2003, Ruston and Humphries 2003, Jackson et al. 2004), but also relate the extent of such movement to the magnitude of utility differences among patches. In classical IFD models, foragers are assumed always to move to the best patch, i.e., to the one patch that provides them with the highest resource intake rate. This unrealistic assumption results in the prediction of classical IFD theory that, at the IFD, foragers enjoy identical intake rates across all patches. In the real world, however, the habitat-choice behaviour of foragers is never perfect, although natural selection might have shaped it surprisingly well. It is instead reasonable to assume that foragers make increasingly more errors in patch choice when differences in the involved patch utilities are small. We therefore incorporated this more realistic assumption into our model. Accordingly, our model predicts all patches to host at least some foragers (even if their quality is extremely low), so that the resultant distribution of foragers at equilibrium is less skewed than predicted by IFD theory. Our results agree with findings from previous theoretical studies that tried to overcome the unrealistic assumption of optimal movements by complementing them with a fixed proportion of random movements (Houston and McNamara 1987). These models thus combined two unrealistic types of movement, fully optimal and fully random movement, to achieve a greater degree of realism in the description of forager movement. We believe that our model of sub-optimal movement, according to which movements between any two patches probabilistically depend on their utility difference, offers a considerably more plausible description of real movement processes than either the optimal choice assumed by classical IFD theory or the simple mixture between fully optimal and fully random choice assumed in more recent models.

This greater degree of realism is critical if model analyses are to unravel determinants of forager distributions, or match empirical observations, in real systems.

In our model, the effects of information uncertainty on the distribution of foragers depend on whether these foragers move between patches optimally or sub-optimally. Under optimal movement, information uncertainty does not alter the distribution of foragers. However, under the more realistic non-IFD assumption that the accuracy of patch choice is related to differences in patch utility, increased uncertainty about a patch's utility results in a more uniform distribution of foragers across resource patches than predicted by classical IFD theory. This confirms and extends results of two earlier studies that assumed different types of constrained knowledge about resource utility. In the perceptual-constraints model (Abrahams 1986), foragers cannot distinguish between differences in patch utilities that are smaller than a certain threshold. Ranta et al. (1999, 2000) instead assumed knowledge of foragers about patch utilities to be limited to neighbouring patches, located within a certain distance of their current patch. Our analyses go beyond these earlier approaches in three important respects. First, we explicitly distinguish errors in perception (modelled in terms of information uncertainty about patch utility) from errors in implementation (modelled in terms of sub-optimal patch choice), which together must be expected to affect all realistic foraging behaviours. Our study reveals the effects of both types of error acting in separation and conjunction. Second, we allowed the perceived utility differences and the implemented foraging movements between patches to vary gradually with patch utilities, thus avoiding the typically implausible assumption of foraging behaviour changing abruptly as utility differences between patches shrink. Third, we incorporated the fact that in realistic settings the certainty about the resource utility of a given patch will tend to decrease gradually with the distance from a forager's current patch, thus avoiding the typically implausible assumption of information certainty changing abruptly as distances between patches grow.

Perhaps most strikingly, we found that, when movement is sub-optimal, travelling cost among patches lead to forager distributions that increasingly resemble those predicted by classical IFD theory. At first glance, this novel finding would appear to conflict with Åström's (1994) conclusion that the cost of travelling between patches does not have a consistent effect on the distribution of foragers among patches. This conflict is only apparent, since our results agree with his conclusion as long as we follow his other assumption that foragers move between patches optimally ($\alpha \to \infty$). However, when foragers move among patches sub-optimally, in accordance with the difference in patch utility ($\alpha < \infty$), which is a more realistic assumption as previously mentioned, travelling costs have a consistent impact on the distribution of foragers, which indeed contradicts Åström's (1994) conclusion. To our surprise, the distribution of foragers becomes more skewed and approaches the IFD as travelling costs increase. We suggest that our findings on the impact of travelling costs on the distribution of foragers are of particular ecological interest, because this impact works in the opposite direction of other realistic aspects ignored in the classical IFD theory (e.g., competitive abilities among foragers, as reviewed in Tregenza 1995, or sub-optimal movement and information uncertainty, as examined in this study).

Why does the distribution of sub-optimal foragers approach the IFD with increasing travelling costs? In our model, foragers keep moving between patches even when the forager distribution is at equilibrium (Houston and McNamara 1987), due to our realistic assumption of sub-optimal movement between patches. At this type of dynamic equilibrium, the number of foragers entering a patch by definition equals the number of foragers leaving the same patch. Let us consider a pair of patches of high (R) and low (P) quality, and assume that there are no costs of travelling. When patch R hosts more foragers than patch P, and intake rates are equal in both patches, half of the foragers in patch R are expected to move to patch P, while the other half stays in patch R (see Fig. 1 a; the probability of choosing patch P is 50% when the utility difference between the two patches is 0). The same applies to patch P. Accordingly, the actual number of emigrants from R to P exceeds the number of emigrants from P to R, because patch R hosts more foragers than patch P. The number of foragers in patch P thus increases, and the dynamic of forager movement reaches equilibrium when the number of emigrants from R and P becomes equal. At equilibrium, patch P thus hosts more foragers than it does in the IFD. This is a mechanistic explanation why, without travelling costs, the distribution of sub-optimal foragers is less skewed than classical IFD theory predicts. When travelling costs exist, the number of foragers that move to the other patch is diminished, because the utility of the other patch is reduced by the travelling cost. The rate of this decline in the number of emigrants from the high-quality patch R to the low-quality patch P is larger than that from P to R (Fig. 2 a; the decline rate would be equal only if the curve were exponential). Therefore, the number of foragers in the high-quality patch R increases. This asymmetry caused by travelling costs shifts the equilibrium distribution closer to the IFD, and does so there more the larger those costs.

Why did previous theoretical investigations fail to find this effect? Two explanations come to mind. To understand the first potential explanation, we must recall that the forager distribution does not approach a single equilibrium when foraging movements are optimal ($\alpha \to \infty$) and travelling costs are smaller than the benefit experienced through the intake of resources. If travelling cost exceeds that benefit, optimal foragers stop moving at some stage, resulting in different endpoints within the equilibrium ranges shown in Fig. 4. Most of the existing simulation models on the impact of travelling costs provided predictions on moving frequency (Regelman 1984) and prey mortality (Bernstein et al. 1991, Kacelnick et al. 1992), but made no explicit prediction on the distribution of foragers. This focus may have resulted from the existence of equilibrium ranges instead of single equilibrium points. To understand the second potential explanation, we must recall that a patch of a certain quality hosts slightly different numbers of foragers at equilibrium, depending on the quality of its neighbouring patches. Both effects make the relationship between patch quality and forager number more complicated, which may help explain why previous studies have failed to report a systematic impact of travelling costs on forager distributions.

To our knowledge, only two experimental studies have empirically tested the effect of travelling costs on departures from the IFD, and both of these have suggested that the introduction of travelling costs increases the proportion of foragers staying in poor patches (Korona 1990, Kennedy and Gray 1997). This would appear to contradict the results of the present study. However, in interpreting these experimental studies we must be aware of several additional factors that might have affected the experiments. For example, in the experiment with free-ranging ducks (Kennedy and Gray 1997), travelling costs were introduced by increasing the distance between two feeding patches. An increase in this distance might decrease the number of foragers currently travelling between the two patches, and thus increase the number of foragers currently staying in the two patches. In the context of our model, this is equivalent to increasing the total number of foragers, which, as we have shown above, results in a more uniform forager distribution, in line with the experimental observations. Another possible side effect of increasing the distance between two feeding patches is a reduced accuracy of discriminating the two patch utilities, which, according to the perceptual-constraints models (Abrahams 1986) and our own results, makes the forager distribution less skewed, again in line with the experimental observations.

Our model results address the case of a forager population of constant size exploiting a constantly renewing spatially structured resource. Thus, the number of foragers in a given patch increases exclusively due to immigration, instead of through enhanced reproduction and/or survival. The opposite extreme assumption is that foragers do not move between patches at all, but experience different reproduction and/or survival rates in different patches, which can also lead to an IFD (Cressman and Křivan 2006). Thus, an IFD is attainable through qualitatively different mechanisms, and the present study considered forager movement instead of forager demography. Situations in which forager movement is fast compared with forager demography are characteristic, for example, of birds exploiting spatially structured resources such as insects or fish. Fast forager movement, as compared to slow forager demography, also applies to humans such as commercial fishers or recreational anglers that exploit fish populations distributed across lakes or patchy marine habitats (Parkinson et al. 2004). Our results based on a general logistic growth model of resource dynamics also demonstrate that forager distributions are quantitatively affected by the type of heterogeneity considered among resource patches, i.e., by whether variability among patches exists in carrying capacities or intrinsic growth rates. These observations imply that the relative timescales of forager movement and demography, as well as the type of resource variability across patches, need to be carefully considered when empirical observations are interpreted in the light of our results.

Predictions and assumptions of the original and extended IFD models have been tested in many empirical studies using a variety of animal taxa (reviewed in Tregenza 1995), including humans (Abrahams and Healey 1990, 1993, Gillis et al., 1993, Gillis

2003, Abernethy et al. 2007). Besides such empirical tests of predictions by IFD theory, some authors have incorporated IFD principles into theoretical models as basic assumptions and investigated their consequences on predator-prey dynamics, in efforts to obtain insights for resource management (e.g., Dolman and Sutherland 1997, Parkinson et al. 2004). Our study here suggests that predictions based on the original IFD model might be misleading if, for example, foragers experience travelling costs and information uncertainty, or if they move sub-optimally instead of optimally. Our model removes some of the most serious over-simplified assumptions of classical IFD theory, while generating general and robust findings about the resultant departures from IFD predictions. Although our model is based on quite general assumptions for the demography of foragers (constant numbers) and resources (logistic growth with exploitation), it is flexible enough to allow extensions through the incorporation of more complex forager and resource dynamics. The present model can also be developed further as the basis for a comprehensive and systematic investigation of factors influencing the distribution of foragers in space. For example, Parkinson et al. (2004) assumed that recreational anglers follow an IFD across a landscape of lakes, resulting in identical catch rates at equilibrium. Based on this assumption, they predicted systematic overexploitation of high-quality lakes. In the light of our results, it seems important to test to what extent this or other conclusions derived from classical IFD assumptions hold when accounting for sub-optimal movement, information uncertainty, or travelling costs. Our general model introduced here may thus serve as a starting point for analysing more complex forager distributions.

What types of experimental studies are required to test the predictions from the present study? As already mentioned, information uncertainty and travelling costs are often confounded in empirical studies; it is therefore important to separate these two factors. To test the effects of travelling costs on forager distributions, for example, introducing an additional cost to travelling, such as predation risk, might be a promising approach. Experimenters might also be able to force foragers to experience different effective distances for information acquisition and travelling, for example, by using a two-patch system in which foragers can learn about the utility of the other patch by directly observing it (short distance), even though they need to make a detour to reach it (long distance). The vast majority of previous experimental tests of IFD theory were carried out in laboratories, adopting a simple system consisting of two patches of high and low quality. Using three or more patches (e.g., Carter and Abrahams 1987) and altering the distances among them would therefore be important in the future. Although it is sometimes difficult to control for all factors affecting the distribution of foragers, well-designed field experiments or observations are needed to elucidate general patterns resulting from information uncertainty and travelling costs. In such situations, quantifying key variables in the model – in particular, the quality of resource patches, information that foragers possess, and the costs of travelling – is important for testing the predictions from our study. For example, foragers might be followed for extended periods of time using novel biotelemetry methods. Promising future research also includes systematic investigations of so far unexplored factors affecting forager distributions in space and time, in particular, the remaining three out of seven categories of over-simplifying assumptions in classical IFD theory (Tregenza 1995) could fruitfully be addressed (fixed resources in space and time, rate of resource intake as the only factor affecting the patch choice of foragers, and distribution of foragers determined entirely by maximizing their short-term fitness).

In conclusion, here we have unravelled the consistent effects of three simplifying assumptions of traditional IFD theory on the distribution of foragers. The robustness of our findings is underscored by their consistency for two-patch and multi-patch models, and also for variability among patches in terms of carrying capacities and intrinsic growth rates. While simple models like those used in classical IFD theory are of great value for explaining broad and general patterns in behavioural ecology, their extension and generalization are useful for obtaining deeper insights and more adequate predictions. In particular, our model has demonstrated the previously unrecognized effects of travelling costs on the distribution of sub-optimal foragers, as well as the consistent impacts of sub-optimal movement and information uncertainty on departures from IFD predictions. We hope that our results will encourage experimental studies of these three factors, and will ultimately contribute to a better understanding of forager behaviour across spatially structured resources.

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Appendix

Here we present an analytical examination of the ideal free distribution (IFD) of foragers when the carrying capacity K or the intrinsic growth rate r varies between patches, either separately or jointly. Our goal is to derive the relationships between the forager numbers and the values of K or r characterizing patches at the IFD equilibrium.

At the IFD, the resource is at equilibrium in each patch $i = 1, \ldots, n$,

$$r_i(1 - R_i^* / K_i) - qF_i^* = 0,$$

and foragers experience the same intake rate V^* across all patches,

$$V^* = R_i^*\{1 - \exp(-qF_i^*)\} / F_i^* = K_i(1 - qF_i^* / r_i)\{1 - \exp(-qF_i^*)\} / F_i^*.$$

Using the Taylor expansion $\exp(-qF_i^*) \approx 1 - qF_i^*$, which is valid when foraging is mild ($qF_i^* \ll 1$ or $q \ll 1/F_i^*$), we obtain

$$V^* = K_i(1 - qF_i^* / r_i)q$$

and therefore

$$F_i^* = r_i(q^{-1} - q^{-2}V^*K_i^{-1}).$$

This shows that when carrying capacities are constant across patches, $K_i = K$, the relationship between F_i^* and r_i is linear, $F_i^* \propto r_i$. When instead intrinsic growth rates are constant across patches, $r_i = r$, the relationship between F_i^* and K_i is concave from below, approaches a maximum of $F_i^* = r / q$ for $K_i \to \infty$, and is negative for $K_i < V^* / q$, which means that patches with carrying capacities below V^* / q remain empty of foragers. Since an increase in the total forager number F_{tot} causes a decrease in V^*, and thus in the threshold V^* / q, the number of empty patches decreases when there are more foragers in total. While our simulation results shown in Fig. 5 are based on the specific assumption of the quality of the 100 patches following a normal distribution, we have thus confirmed that our conclusions about (i) the different impacts of variability among patches in either carrying capacities or intrinsic growth rates and about (ii) the impacts of the total forager number are both valid more generally.

Table

Table 1. Parameters and variables used in this study.

Symbol	Description		Default value (range)
	Parameters		
n	Number of patches	in two-patch model	2
		in multi-patch model	100
K_i	Carrying capacity of resource in patch i		mean = 600
r_i	Intrinsic growth rate of resource in patch i		mean = 0.3
α	Movement optimality of foragers		1, 5, or ∞ $[0, \infty)$
T_1	Travelling cost of foragers for moving between neighbouring patches		0 $[0, \infty)$
I_1	Information certainty of foragers about neighbouring patches		1 [0, 1]
ϕ_1	Information uncertainty of foragers about neighbouring patches ($= 1 - I_1$)		0 [0, 1]
F_{tot}	Total number of foragers	in two-patch model	20 [5, 50]
		in multi-patch model	1000 [200, 2000]
$\bar{F}$	Average number of foragers per patch ($= F_{\text{tot}} / n$)		10
q	Foraging rate		0.01
	Variables		
R_i	Resource abundance in patch i		n.a.
F_i	Forager abundance in patch i		n.a.
V_i	Per capita resource intake rate of foragers in patch i		n.a.
U_{ij}	Utility of patch j as viewed from patch i		n.a.
M_{ij}	Probability of moving from patch i to patch j		n.a.
d_{ij}	Distance between patch i and patch j		n.a.

Figure captions

Fig. 1. Schematic illustration of assumptions used in our model. We relax three assumptions of the classical IFD model, i.e., (i) optimal foraging moves among patches, (ii) perfect information about the utility of resource patches, and (iii) cost-free travelling between patches. In the classical IFD model, foragers always choose the foraging patch that offers the highest resource intake rate. In the present model, the patch choice of foragers is assumed to depend on the utility difference between patches, with the degree of movement optimality being controlled by the parameter α (a). As α increases, patch choice approaches optimal foraging. Furthermore, in the present model the knowledge of foragers about the resource utility in other patches is assumed to decline with distance (b), while travelling costs between patches are assumed to increase with distance (c). As parameters $\phi_1 = 1 - I_1$ and T_1 decrease, conditions approach those assumed in the classical IFD model.

Fig. 2. Impacts of movement optimality α on the proportion of foragers in the poor patch (a, b) and on their intake rates (c, d) in the two-patch model. The two left panels (a, c) show the case when the two patches differ in their carrying capacities (K_P = 400, K_R = 800, r_P = r_R = 0.3), while the two right panels (b, d) show the case when the two patches differ in their intrinsic growth rates (K_P = K_R = 600, r_P = 0.2, r_R = 0.4). In panels (c) and (d), solid and dashed lines show intake rates in the rich and poor patches, respectively, while dotted lines in all panels show IFD predictions.

Fig. 3. Impacts of the total number of foragers and of the disparity in patch quality on the proportion of foragers in the poor patch (a–d) and on their intake rates (e–h) in the two-

patch model. The four left panels (a, c, e, g) show the case when the two patches differ in their carrying capacities (K_P = 400, K_R = 800, r_P = r_R = 0.3), while the four right panels (b, d, f, h) show the case when the two patches differ in their intrinsic growth rates (K_P = K_R = 600, r_P = 0.2, r_R = 0.4). Dotted lines show IFD predictions ($\alpha \to \infty$), while black and grey lines show the cases $\alpha = 1$ and $\alpha = 5$, respectively. In panels (e–h), solid and dashed lines show the intake rates in the rich and the poor patch, respectively.

Fig. 4. Impacts of information uncertainty (a, d) and travelling costs (b, e) on the proportion of foragers in the poor patch (upper panels) and on their intake rates (lower panels) in the two-patch model. The two patches differ in their carrying capacities (K_P = 400, K_R = 800, r_P = r_R = 0.3). Dotted lines show IFD predictions ($\alpha \to \infty$), while black and grey lines show the cases $\alpha = 1$ and $\alpha = 5$, respectively. In panels (d) and (e), solid and dashed lines show the intake rates in the rich and the poor patch, respectively. The shaded areas in panels (b) and (e) show the equilibrium ranges in which optimal foragers ($\alpha \to \infty$) do not move between patches. Panel (c) shows, for $\alpha = 1$, interactions between information uncertainty and travelling costs in their joint effect on the proportion of foragers in the poor patch. The IFD proportion is 0.134.

Fig. 5. Impacts of the total number of foragers and of movement optimality on the distribution of foragers and their intake rates in the multi-patch model when patches differ in their carrying capacities (left) or in their intrinsic growth rates (right). Each point represents the value in a single patch. The total number of foragers is 200, 1000, or 2000, which corresponds to $\bar{F} = 2$ (squares), $\bar{F} = 10$ (circles), or $\bar{F} = 20$ (diamonds), respectively. Movement optimality α is ∞ (IFD, dotted lines), 5 (grey symbols), or 1 (black symbols). IFD intake rates ($\alpha \to \infty$) are not shown for patches that host no foragers.

Fig. 6. Impacts of information uncertainty and travelling costs on the distribution of foragers and their intake rates in the multi-patch model when patches differ in their carrying capacities. Dotted lines show IFD predictions ($\alpha \to \infty$), while black circles and triangles show the case α = 1. Each circle or triangle shows the value in a single patch. In panels (a) and (d), the information uncertainty ϕ_1 is varied from 0.0 (circles) to 0.5 (triangles). In panels (b) and (e), the travelling cost T_1 is varied from 0.0 (circles) to 2.0 (triangles). Similar changes are found when α = 5 (results not shown). IFD intake rates ($\alpha \to \infty$) are not shown for patches that host no foragers. Since a patch of given quality hosts slightly different numbers of foragers at equilibrium, depending of the quality of its neighbouring patches, the relative position of all patches are randomized between simulations and shown values are averaged over 100 simulations. Panel (c) shows, for $\alpha = 1$, interactions between information uncertainty and travelling costs in their joint effect on the proportion of foragers in the poorest patch. The number of foragers in the poorest patch is shown relative to the average number of foragers per patch ($\bar{F} = 10$). The IFD proportion is exactly 0.

Fig. 7. Impacts of the spatial autocorrelation between the resource qualities of neighbouring patches on the distribution of foragers in a multi-patch model with 100 patches located along a one-dimensional ring. The autocorrelation coefficient of carrying capacities of adjacent patches is varied between –0.9 and +0.9. The number of foragers in the poorest patch is shown relative to the average number of foragers per patch ($\bar{F} = 10$). As in Fig. 6, shown values are averaged over 100 simulations.

Fig. 1

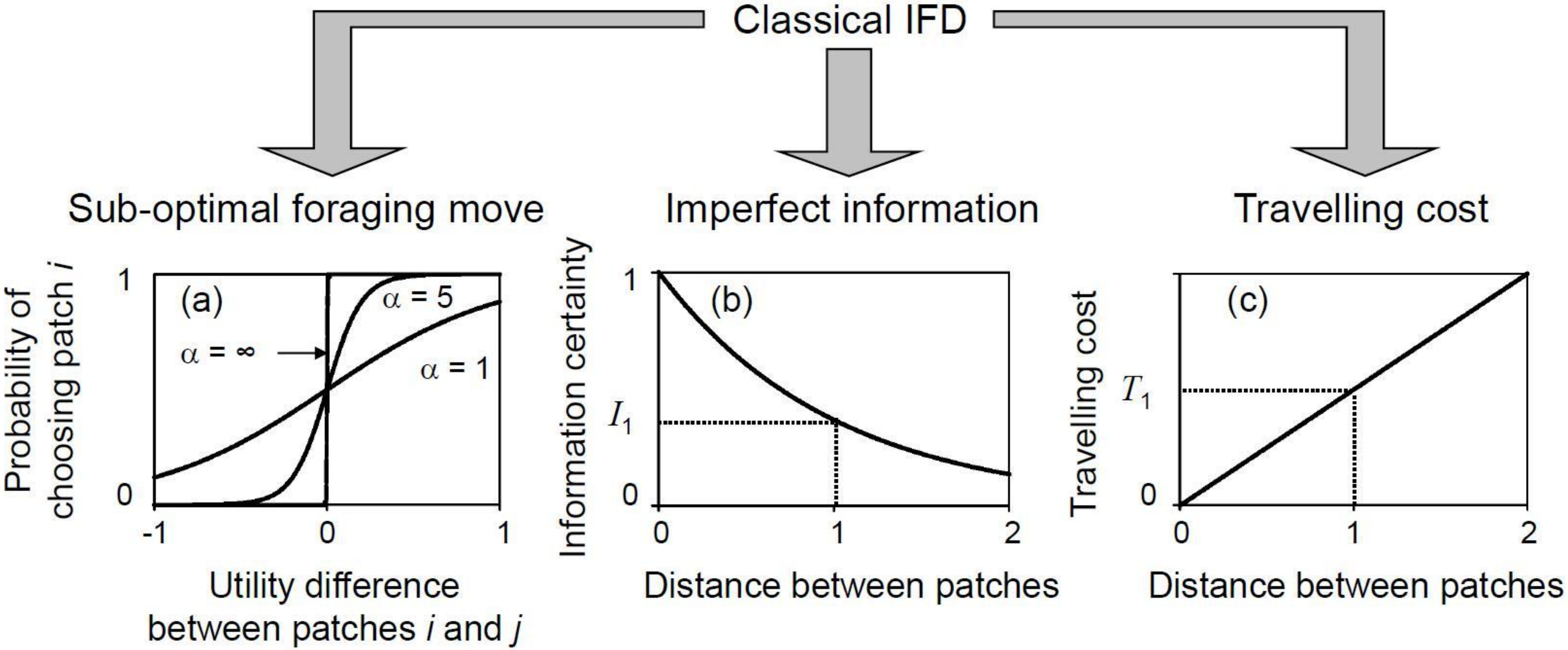

Classical IFD
Sub-optimal foraging move
Imperfect information
Travelling cost
(a)
Probability of choosing patch i
1
0
$\alpha = 5$
$\alpha = \infty$
$\alpha = 1$
-1
0
1
Utility difference between patches i and j
(b)
Information certainty
1
I_1
0
0
1
2
Distance between patches
(c)
Travelling cost
T_1
0
0
1
2
Distance between patches

Fig. 2

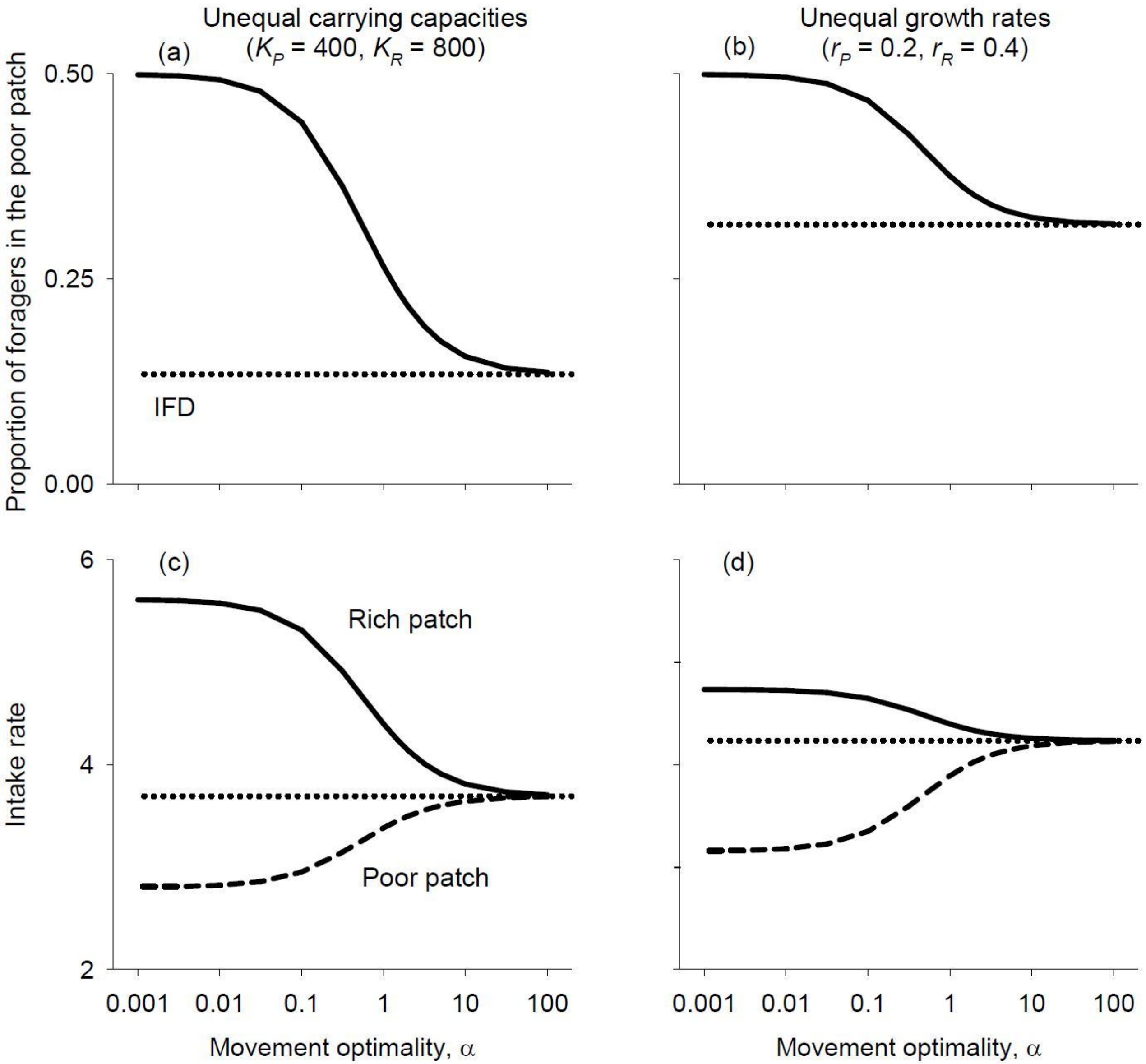
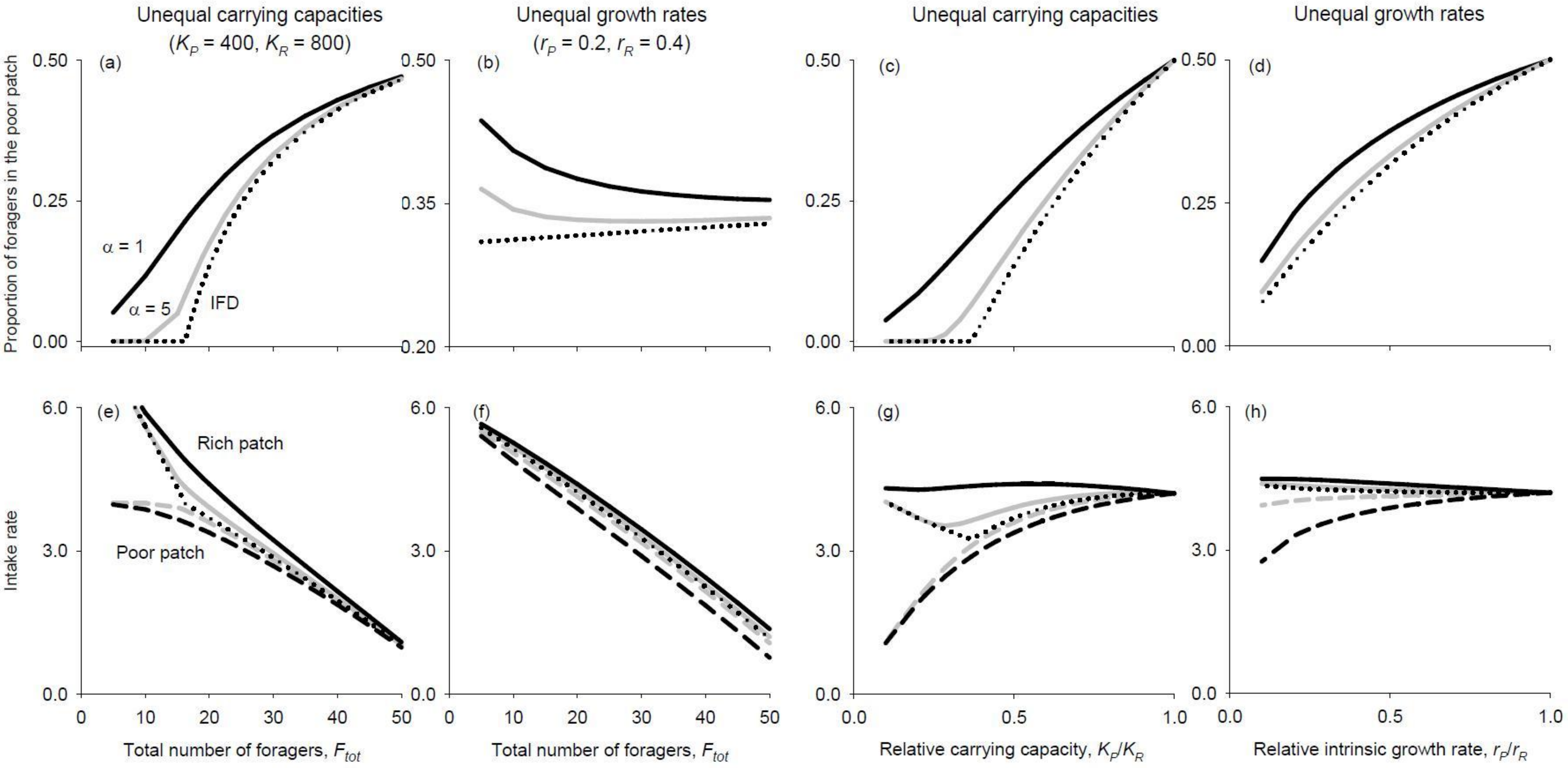

Unequal carrying capacities
(K_P = 400, K_R = 800)
Unequal growth rates
(r_P = 0.2, r_R = 0.4)
(a)
(b)
(c)
(d)
Proportion of foragers in the poor patch
0.50
0.25
0.00
IFD
Intake rate
6
4
2
Rich patch
Poor patch
0.001
0.01
0.1
1
10
100
Movement optimality, α

Fig. 3



Unequal carrying capacities
(K_P = 400, K_R = 800)
Unequal growth rates
(r_P = 0.2, r_R = 0.4)
Unequal carrying capacities
Unequal growth rates
Proportion of foragers in the poor patch
(a)
(b)
(c)
(d)
α = 1
α = 5
IFD
0.50
0.25
0.00
0.35
0.20
Intake rate
(e)
(f)
(g)
(h)
Rich patch
Poor patch
6.0
3.0
0.0
0
10
20
30
40
50
0.5
1.0
Total number of foragers, F_{tot}
Total number of foragers, F_{tot}
Relative carrying capacity, K_P/K_R
Relative intrinsic growth rate, r_P/r_R

Fig. 4

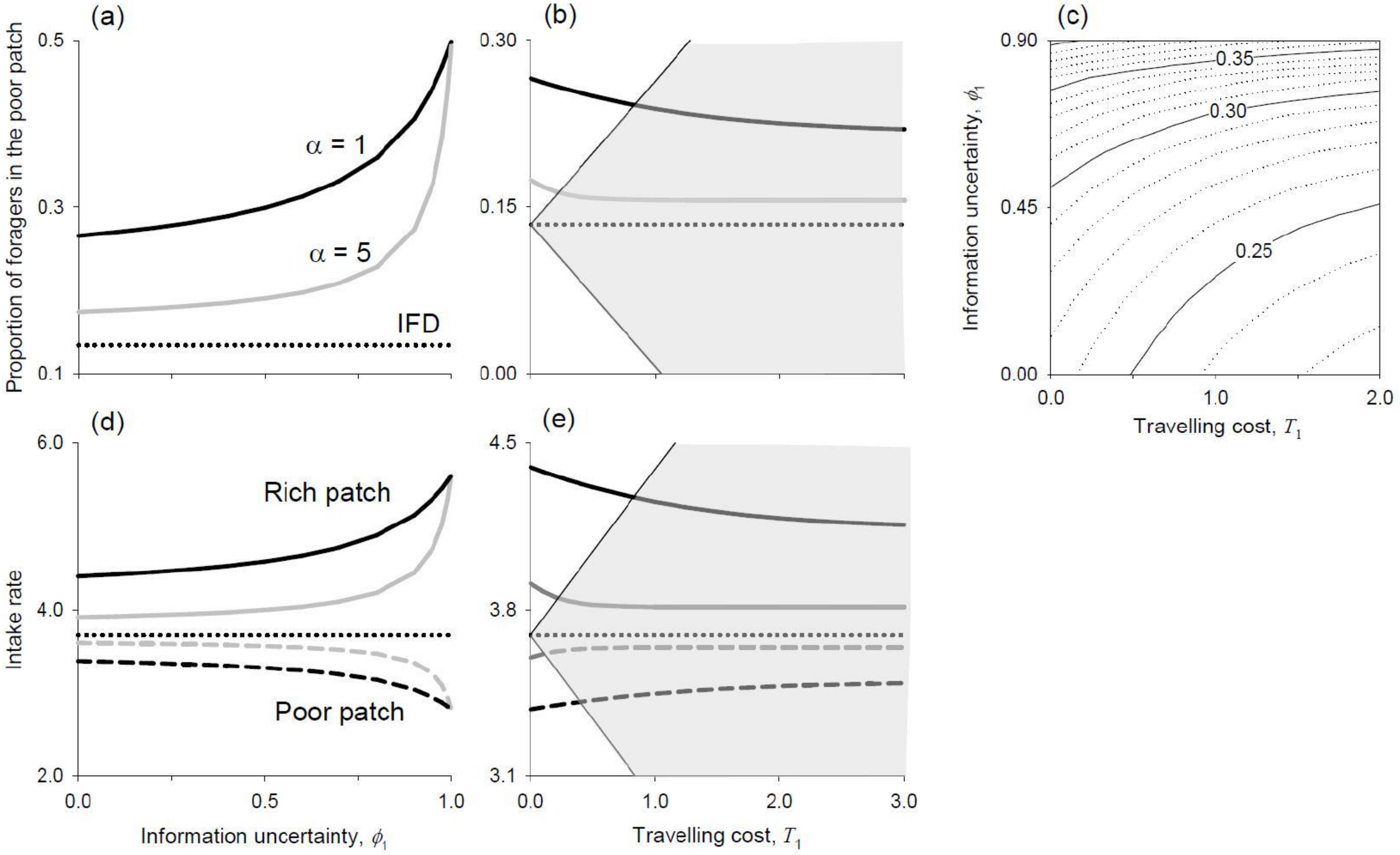

(a)
(b)
(c)
Proportion of foragers in the poor patch
0.5
0.3
0.1
α = 1
α = 5
IFD
0.30
0.15
0.00
0.90
0.45
0.00
0.35
0.30
0.25
Information uncertainty, ϕ_1
0.0
1.0
2.0
Travelling cost, T_1
(d)
(e)
Intake rate
6.0
4.0
2.0
Rich patch
Poor patch
4.5
3.8
3.1
0.0
0.5
1.0
Information uncertainty, ϕ_1
0.0
1.0
2.0
3.0
Travelling cost, T_1

Fig. 5

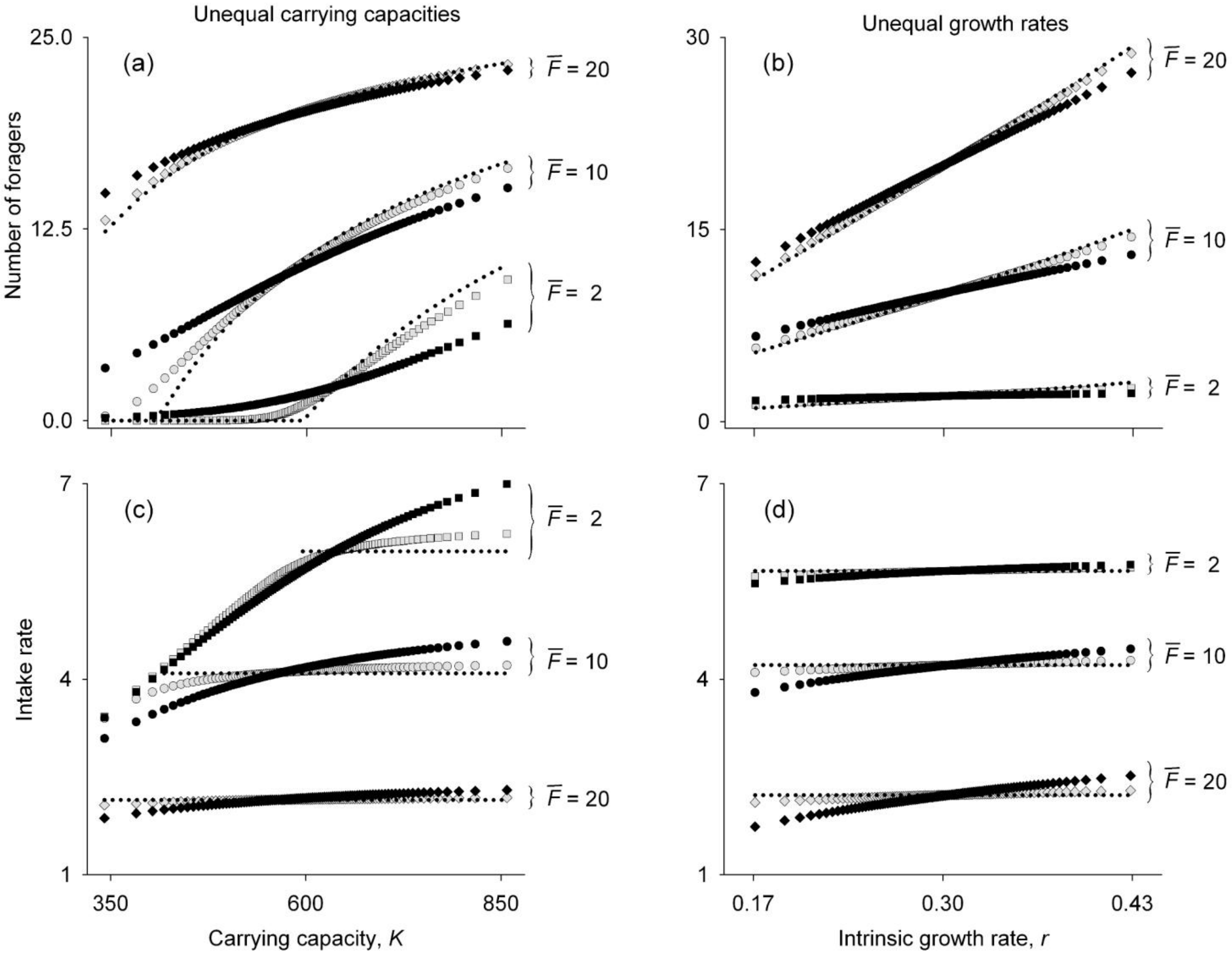

Unequal carrying capacities
Unequal growth rates
(a)
(b)
(c)
(d)
Number of foragers
Intake rate
25.0
12.5
0.0
30
15
0
7
4
1
350
600
850
0.17
0.30
0.43
Carrying capacity, K
Intrinsic growth rate, r
$\overline{F}$ = 20
$\overline{F}$ = 10
$\overline{F}$ = 2

Fig. 6

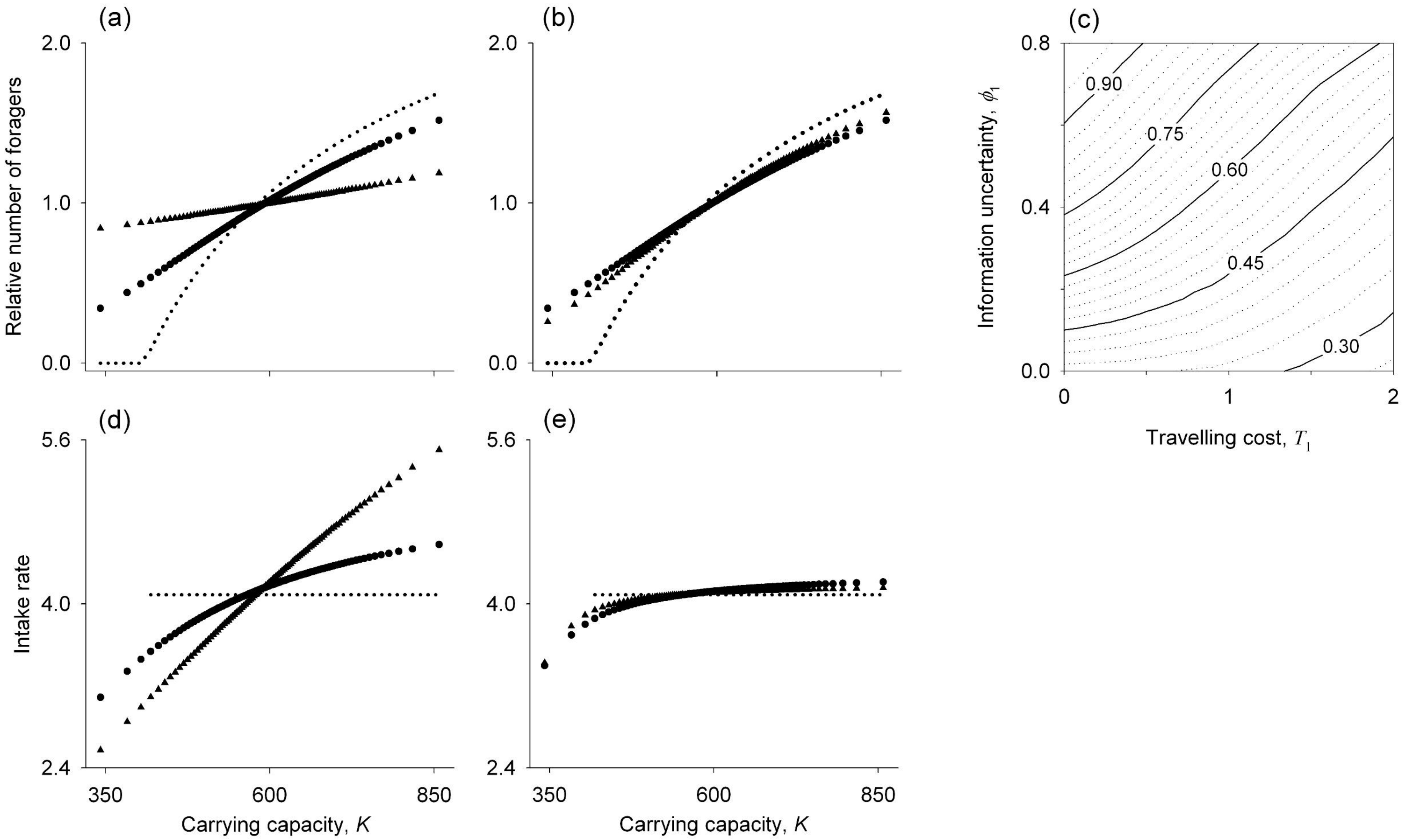
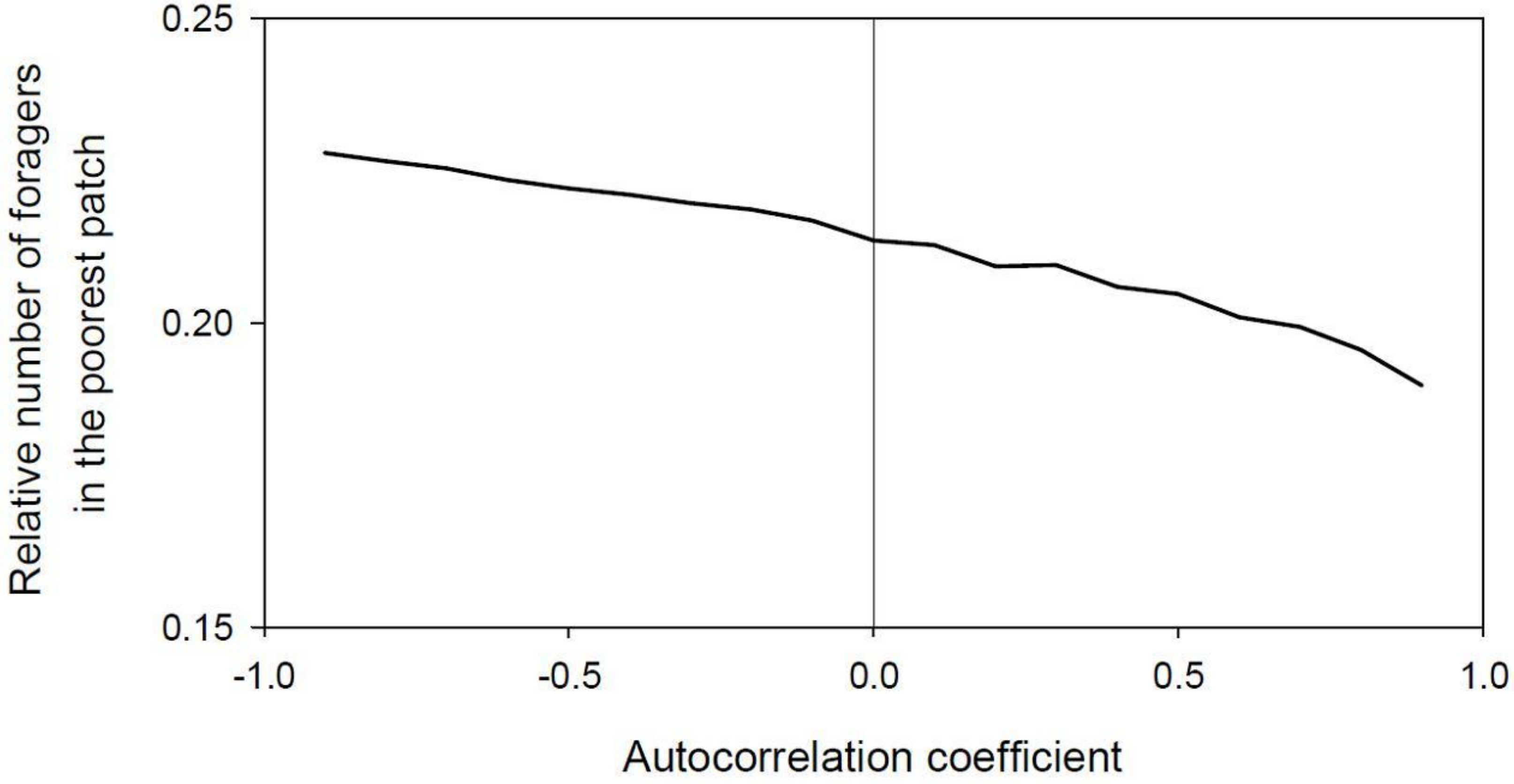

(a)
(b)
(c)
(d)
(e)
Relative number of foragers
2.0
1.0
0.0
Information uncertainty, ϕ_1
0.8
0.4
0.0
0.90
0.75
0.60
0.45
0.30
0
1
2
Travelling cost, T_1
Intake rate
5.6
4.0
2.4
350
600
850
Carrying capacity, K

Fig. 7


0.25
0.20
0.15
-1.0
-0.5
0.0
0.5
1.0
Relative number of foragers in the poorest patch
Autocorrelation coefficient