

## Habitat Selection and Predator–Prey Dynamics

In their recent *TREE* article, Kacelnik *et al.*<sup>1</sup> reviewed the Fretwell–Lucas models of ideal free and ideal despotic habitat choice<sup>2,3</sup> and explored the implications for predator–prey dynamics. It ought to be pointed out that what is referred to as ‘the most simple Fretwell–Lucas model’ of ideal free habitat choice is a later modification, containing several assumptions which were not parts of the original model. Contrary to the statements of Kacelnik *et al.*, Fretwell and Lucas did not make any assumptions concerning prey distribution or the relation between prey density and predator fitness. Fretwell and Lucas assumed that all habitats have some basic suitability, which can be measured as the average fitness of its inhabitants at very low population densities. Moreover, they assumed that the suitability of the habitat normally decreases with increasing population density. Whether this is due to intensified resource competition or predation was not specified. The concept of interference competition was not even mentioned by Fretwell and Lucas, nor did they assume that resources are not depleted by consumers (this assumption is in direct conflict with the thrust of Fretwell’s contributions<sup>3–6</sup>, and the approach of the whole MacArthur school, emphasizing indirect competitive interactions via depletion of shared resources).

Tests of the two models should thus focus on the relationship between population density and some measurable parameter that can be associated with fitness (e.g. reproduction, survival or growth). Examples of such studies are Fretwell’s study on field sparrows in temperate North America<sup>3</sup>, Andrén’s study on common jays in Swedish coniferous forests<sup>7</sup> and Power’s study on armored catfish in Panamanian streams<sup>8</sup>.

By themselves, the Fretwell–Lucas models of habitat choice do not generate any predictions on predator–prey interactions, although such predictions can be derived by integrating the models of habitat choice with models of predator–prey interactions. Kacelnik *et al.* do this using primarily a model based on the assumption of strong feeding interference and infinitely high searching efficiency. These premises seem to be realistic when resources are provided at a constant rate in a given spot and overt aggression does not occur<sup>9</sup>. It remains to be seen how common such situations are in nature.

If resources are more evenly distributed, searching costs will count.

Thus, even in systems with feeding interference, intake rates will depend on both predator–prey ratios and absolute prey densities. In systems without substantial interference, the fitness of predators will only depend on absolute prey densities (this assumption is routinely made in mechanistic competition models<sup>10–12</sup>). In explicit predator–prey models, an assumption of purely exploitative competition translates to a vertical predator isocline<sup>13,14</sup>, implying that each habitat with any predators at all will have exactly the same prey density. Increasing productivity will result in higher predator densities, higher rates of prey turnover and higher numerical predator–prey ratios, as was the case in Power’s study of the interaction between armored catfish and stream algae<sup>8</sup>. These predictions are in sharp contrast to the prediction of Kacelnik *et al.* that mortality risk due to predation and the numerical predator–prey ratio will be the same in all habitats.

In systems where territories are actually defended, intruding individuals must weigh the expected fitness within the habitat against the risk of losing territorial contests and the fitness costs of such losses. This will create ideal despotic habitat choice<sup>3</sup>, where the average fitness of predators is positively correlated to the productivity of their habitat. Stable social hierarchies<sup>15</sup> and pre-emptive competition for territories<sup>16</sup> have a similar impact. At equilibrium, all these mechanisms create source–sink dynamics<sup>16</sup>, where the best habitats are characterized by net emigration and the poorest habitats are characterized by net immigration. In predator–prey models, net emigration implies a rightwards curved predator isocline, whereas net immigration creates a hyperbolic predator isocline, which meets the predator axis above the origin<sup>17</sup>. In such predator–prey systems, the relationship between predation pressure and the productivity of the habitat is ambiguous and depends, for example, on the abundance relationships between different habitat types in the landscape and on the reproductive potential of the prey in different habitats<sup>17</sup>.

In the last sections of their article, Kacelnik *et al.* discuss systems with positive search costs, exploitation competition and second-degree predation. The article creates the impression that these modifications are at variance with the original model. However, similar predictions have been derived by integrating the two models of habitat choice with

Rosenzweig-type models of predator–prey interaction<sup>5,16</sup>. The results are thus consistent with the Fretwell–Lucas models of ideal free and ideal despotic habitat choice.

### Tarja Oksanen

Dept of Animal Ecology, University of Umeå,  
S-901 87 Umeå, Sweden

### Lauri Oksanen

Dept of Ecological Botany, University of Umeå,  
S-901 87 Umeå, Sweden

### Stephen D. Fretwell

Seven Oaks Academy, Route 1, Box 328, High  
View, WV 26808, USA

### References

- 1 Kacelnik, A., Krebs, J.R. and Bernstein, C. (1992) *Trends Ecol. Evol.* 7, 50–55
- 2 Fretwell, S.D. and Lucas, H.L., Jr (1969) *Acta Biotheor.* 19, 16–36
- 3 Fretwell, S.D. (1972) *Populations in a Seasonal Environment*, Princeton University Press
- 4 Fretwell, S.D. (1977) *Perspect. Biol. Med.* 20, 169–185
- 5 Oksanen, L., Fretwell, S.D., Arruda, J. and Niemelä, P. (1981) *Am. Nat.* 118, 240–261
- 6 Fretwell, S.D. (1987) *Oikos* 50, 291–301
- 7 Andrén, H. (1990) *Ecology* 71, 1769–1803
- 8 Power, M. (1984) *J. Anim. Ecol.* 53, 357–374
- 9 Milinski, M. (1988) *Trends Ecol. Evol.* 3, 325–330
- 10 MacArthur, R.H. (1972) *Geographical Ecology*, Harper & Row
- 11 Tilman, D. (1982) *Resource Competition and Community Structure*, Princeton University Press
- 12 Holt, R. (1983) *Am. Nat.* 122, 521–541
- 13 Rosenzweig, M.L. (1971) *Science* 171, 385–387
- 14 Rosenzweig, M.L. (1977) *Q. Rev. Biol.* 52, 371–380
- 15 Lomnicki, A. (1978) *J. Anim. Ecol.* 47, 461–475
- 16 Pulliam, H.R. and Danielsson, B. (1991) *Am. Nat.* 137S, 50–66
- 17 Oksanen, T. (1990) *Evol. Ecology* 4, 220–234

## Reply from Kacelnik, Bernstein and Krebs

Oksanen *et al.* object to some points in our recent review of ideal free distribution models. Some of the issues they raise are terminological and result from our attempt to relate recent work to Fretwell’s original work. They state that the Fretwell–Lucas model did not make any assumptions about prey distribution or about the relation between prey density and predator fitness. They also point out that interference was not mentioned. In fact, they refer to ‘habitats’ with different ‘basic