Evolutionary Ecology Research, 2002, **4**: 471–493

The ideal free distribution: an analysis of the perceptual limit model

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ABSTRACT

Since the introduction of the ideal free distribution in the 1970s, amendments have attempted to explain observations that deviate from the prediction of input matching. We consider a perceptual limit model that relaxes the assumption that animals are ideal. Under the model, individuals move to the location with the highest potential intake rate, unless the potential intake rates differ by less than some fixed amount, in which case the animals move at random. The random movements of the animals mean that there are often many feasible distributions. Here we present a new method of implementing the model in which we treat movements between the feasible distributions as a Markov chain. Analysis of this model shows that the range of feasible distributions is determined by the limits on the random movements of the animals. This new method allows us to compute the equilibrium probability of observing each feasible distribution, to compute the expected long-term rate of intake overall and on each site, and to compute differences in the expected total intake of individual animals depending on their initial site and the initial number on that site. We show that observed limits from feeding trials could be used to provide a more robust test of the perceptual limit model than comparing predicted average distributions.

Keywords: ideal free distribution, input matching, Markov chain model, perceptual limit.

INTRODUCTION

The ideal free distribution (IFD) was developed by Fretwell and Lucas (1970) and Fretwell (1972) to describe how animals distribute themselves among habitats that differ in quality (for reviews, see Milinski and Parker, 1991; Tregenza, 1995; Giraldeau and Caraco, 2000). In the basic model, identical animals have complete knowledge of their environment (i.e. are ideal) and are free to move to the habitat that offers the highest fitness gains. Solitary animals would prefer the highest quality habitat, but the presence of competitors reduces the achievable fitness gains. Therefore, as the total number of animals increases, more animals use the lower quality habitats. In terms of foraging animals, a stable distribution results when no animal can increase its intake rate by switching to an alternative site. Parker

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(1978) showed that for a continuous input scenario where all food items are eaten, the stable distribution is found when the ratio of the number of animals approximates the ratio of the input rates at the two sites. This distribution is known as 'input matching'. Several feeding experiments using fish (Milinski, 1979, 1984; Godin and Keenleyside, 1984) and ducks (Harper, 1982; Gray and Kennedy, 1994) found distributions approximating those predicted by input matching. However, in most of these experiments, the good sites were underused when compared with the predictions of input matching. In addition, some individuals consistently achieved higher intake rates than others, suggesting that the animals were of unequal competitive abilities. Several authors have used the term 'under-matching' for the underuse of the best site when compared with the predictions of input-matching (e.g. Abrahams, 1986; Kennedy and Gray, 1993), but this may lead to confusion with the use of the term to denote deviation from the matching law (Herrnstein, 1970; Baum, 1974, 1979).

In this paper, we are interested in the amendment to the ideal free distribution proposed by Abrahams (1986). He suggested that animals are not ideal and may not be able to distinguish between potential intake rates that are very similar. He proposed the perceptual limit model to incorporate such mistakes in decision making. In the perceptual limit model, individuals move at random between sites if the difference in potential intake rates per unit time is no greater than some given value, the perceptual limit. Abrahams (1986) and Cartar and Abrahams (1997) implemented this model using Monte Carlo simulations of identical animals distributing themselves between various locations. Each run of the simulation gives a distribution in terms of the number of animals on a location and the result is the average of distributions from repeated runs. Here we present a new method of implementing the model. We treat movements between the feasible distributions as a Markov chain and hence derive exact formulae for the equilibrium probability of observing each feasible distribution under our model. Moreover, the model allows us to compute the expected number on each site, the expected long-term rate of intake – both overall and on each site – and to compute differences in the expected total intake of individual animals depending on their initial site and the initial number on that site.

BASIC IFD FRAMEWORK

In the basic model, all animals have the same competitive ability. There is an input of food to two locations. The input rate per unit time at location A is r_A and the input rate at location B is r_B. Food at a location is shared equally between all competitors at that location and all food is eaten. For the distribution of animals to satisfy the ideal free distribution, no animal can increase its intake rate by switching locations. Let there be N animals in total, with N_A animals on site A and N_B animals on site B. For an animal on site A, the potential gain in intake rate per unit time if it switched to site B, G_{AB}, is given by

$$G_{AB} = \frac{r_B}{N_B + 1} - \frac{r_A}{N_A}$$

For an animal on site B, the potential gain in intake rate if it switched to site A, G_{BA}, is given by

$$G_{BA} = \frac{r_A}{N_A + 1} - \frac{r_B}{N_B}$$

Thus no animal will move when both $G_{AB} \leq 0$ and $G_{BA} \leq 0$, and so the distribution is stable when

$$\frac{r_A(N+1)}{r_A + r_B} > N_A > \frac{r_A N - r_B}{r_A + r_B} \tag{1}$$

where $N = N_A + N_B$. These limits give a range of 1 for the value of N_A. Note that the stable distribution can be approximated by the distribution at which intake rates at both locations are equal, although in general a value satisfying this latter condition will not correspond exactly to an integer number of animals. This approximation gives the equation $r_A/N_A = r_B/N_B = (r_A + r_B)/N$. Rearranging the first two terms, we see that $N_A/N_B = r_A/r_B$. Thus, the distribution is stable when the ratio of the number of animals matches the ratio of the input rates at the two locations. This is the 'input matching rule' of Parker (1978).

PERCEPTUAL LIMIT MODEL

The basic ideal free distribution models assume that individuals have complete knowledge of the potential intake rates at each site. We now relax this assumption and examine the effect of limiting an animal's ability to discern small differences in potential intake rates between sites. Decisions are considered to be made at a series of discrete time points. When the difference in the potential intake rates per unit time is greater than the perceptual limit, L, the animal moves to the site that offers the higher intake rate. When the difference in potential intake rates is less than L, then the animal moves randomly to one of the sites. This is the perceptual limit model of Abrahams (1986). When the difference is exactly equal to L, we will take it that the animal is indifferent between moving and staying, and so is again assumed to move randomly.

In the perceptual limit model, an animal on site A will stay if $G_{AB} < -L$, will move at random (i.e. is equally likely to move or stay) if $-L \leq G_{AB} \leq L$ and will switch to site B if $G_{AB} > L$. Analogous conditions apply to an animal on site B. This type of system has previously been analysed by simulating competitors distributing themselves between sites that differ in resource input rates (Abrahams, 1986; Spencer *et al.*, 1995, 1996; Cartar and Abrahams, 1997). Competitors arrive one at a time and move to the site that offers the higher intake rate, or move at random if the difference between the potential intake rates is less than the perceptual limit. Once all animals have arrived, one competitor at a time is then selected and re-allocated. Re-allocation of competitors is repeated several times. The number of competitors on each site is recorded following every re-allocation and/or following repeated simulations. The average over the various feasible distributions of animals can then be estimated.

It is possible, however, to calculate exactly the equilibrium probability for each feasible distribution of animals, and hence calculate exactly the average distribution. During the initial allocation and first few re-allocations, individuals move to increase their intake rates. However, after a certain point the animals will have distributed themselves so that the intake rates available on the two sites are similar. Thus movements occurring after this point will be random movements. Table 1 shows the advantage of moving to an animal ($N = 10$, $r_A = 14$, $r_B = 6$). Consider first the case $L = 0$. When the gain in intake rate as a result of switching is negative for a site, an animal on that site will not move. If the gain in intake rate is positive, an animal would improve its intake rate by moving to the alternative site. Thus, in the

Table 1. Comparison of potential intake rates

N_A	G_{AB}	G_{BA}
1	-13.40	6.33
2	-6.33	3.92
3	-3.92	2.64
4	-2.64	1.80
5	-1.80	1.13
6	-1.13	0.50
7	-0.50	-0.25
8	0.25	-1.44
9	1.44	-4.60

Note: For an animal on site A, the potential gain in intake rate if it switched to site B is G_{AB}. For an animal on site B, the potential gain in intake rate if it switched to site A is G_{BA}. Animals should switch if the potential change is positive. For example, if there is one animal on site A ($N_A = 1$), an animal on site B would increase its intake rate by switching ($G_{BA} > 0$), but the animal on site A would not ($G_{AB} < 0$). Parameters used are $N = 10$, $r_A = 14$, $r_B = 6$.

example, an animal on site A will move to site B if the number on site A is greater than 7. Similarly, an animal on site B will move to site A if the number on site A is less than 7. Therefore, the only feasible distribution is 7 animals on site A. This distribution is the input matching distribution. If $L = 0.5$, an animal will move at random if the difference is less than or equal to 0.5. Thus, in this example, an animal will move at random from site A to site B if $6 < N_A < 9$ and from site B to site A if $5 < N_A < 8$. Therefore, we have three feasible distributions for $L = 0.5$, $N_A = 6, 7, 8$.

More generally, set $G_{AB}(x) = r_B/(N - x + 1) - r_A/x$ and $G_{BA}(x) = r_A/(x + 1) - r_B/(N - x)$. Then (Appendix 1), the lower minimum number n_L on site A is given by the next integer below the appropriate root of the equation:

$$G_{AB}(x) = -L \tag{2}$$

Similarly, the upper maximum number n_U on site A is given by the next integer above the appropriate root of the equation:

$$G_{BA}(x) = -L \tag{3}$$

These limits can be generalized to include differences in competitive weight (see Lang, 2000).

Given the limits on the feasible distributions of animals, we can model movements within this system, and in particular changes in the number of animals on site A, as a Markov chain (see Appendix 2). Each feasible distribution of animals, defined by the number N_A of animals on site A, corresponds to a state of this chain. The transition probabilities define the probability of the system moving between states. For example, if there are n animals on site A, then a transition increasing N_A (from state n to state $n + 1$) requires an animal on site B to be selected for possible movement; the transition probability is therefore $(N - n)/N$ multiplied by the probability that the selected competitor moves to site A. This probability is 1 if $n < n_L$, 0.5 if $n_L \leq n < n_U$ and 0 if $n \geq n_U$. Similar calculations hold for other transitions (see Appendix 2 for details).

Over time, the probability of being in each of the states in the system will reach an equilibrium value that is independent of time. These equilibrium probabilities for the Markov chain give the probability in equilibrium of observing the corresponding feasible distribution of animals, and hence enable us to calculate the expected value of the number of animals on site A in equilibrium.

We can extend the Markov chain model for aggregate movements to allow us to track the movements of an individual focal animal. In the extended Markov chain, a state has two components: the first component denotes the number of animals on site A and the second component denotes the current site of the focal animal. As before, an animal is selected at random at each time point and uses the perceptual limit model to decide whether to move or stay. The first component of the state will change, as for the basic model, in response to movements by any animal, whereas the second component will change only if the focal animal is selected at that time point and decides to change site. The transition probabilities for this extended Markov chain are given in full in Appendix 3.

Note that the limits on the feasible distributions of animals can also be used to provide the distribution realized when $L = 0$. The model then allows movement when the gains G_{AB} and G_{BA} are exactly zero. Usually, for $L = 0$, we find $n_L = n_U$, so there is just a single integer distribution that satisfies the conditions of the model. However, in cases when $r_A(N + 1)/(r_A + r_B)$ is an integer, the solution of equations (2) and (3) gives $n_L = n_U - 1$ and there will be two feasible distributions. We will sometimes make comparisons with the $L = 0$ distribution(s) rather than the input matching distribution, because input matching gives a real number distribution that can only be realized if the animals can be divided exactly in the same ratio as the resources.

MODEL PREDICTIONS

Characteristics of the model

In our model, as animals are added to the system they either choose the site that offers the higher potential intake rate, or move at random to one of the sites if the difference in the potential intake rates is less than or equal to the perceptual limit, L. Initially, more individuals will choose the site with the higher input rate, thus reducing the potential intake rate available at that site. As noted by Abrahams (1986), from some point onwards all arrivals will choose at random and that point is dependent on the input rates at the two sites. There are, however, also random movements before this point. As each animal moves initially to the site with the higher input rate, the potential intake rate is lowered. At some point it will be indistinguishable from that of the alternative site and so the next animal will move at random. The potential intake rates are again altered and so the next animal may be able to differentiate between the potential intake rates and so may not move at random.

Model predictions for the limits on the feasible distributions

Once all animals have arrived, all movements are random movements within the limits n_L and n_U. These limits on the feasible distributions are determined by the solutions to the equations $G_{AB}(x) = -L$ and $G_{BA}(x) = -L$ and inherit from those equations the following qualitative properties.

(L1) As L increases with the other parameters staying fixed (i.e. as the animals become less discriminating), the lower solution decreases smoothly and the upper solution increases smoothly. Hence n_L decreases and n_U increases as L increases, although the changes are not as smooth because of integer and rounding effects.

(L2) As r_A increases with $r_A + r_B$ and the other parameters fixed (i.e. as site A becomes better), both solutions increase smoothly. Hence n_L and n_U increase as r_A increases, although again not as smoothly.

Table 2 illustrates the limits of the feasible distributions for a range of parameter values similar to those used by Abrahams (1986) and Cartar and Abrahams (1997).

Computations indicate that, for $r_A > r_B$ and for $r_A + r_B$ and the other parameters fixed, the lower solution increases faster with r_A than the upper solution. Essentially, a unit change in

Table 2. Upper and lower feasible limits

			$L = 0$	$L = 0.25$		$L = 1$		$L = 2$		$L = 3$	
(a)	r_A	m	$n_L = n_U$	n_L	n_U	n_L	n_U	n_L	n_U	n_L	n_U
	10	5	5	5	5	4	6	3	7	2	8
	11	5.5	6	5	6	4	7	3	8	2	8
	12	6	6	6	6	5	7	3	8	2	9
	13	6.5	7	6	7	5	8	4	8	3	9
	14	7	7	7	8	6	8	4	9	3	9
	15	7.5	8	7	8	6	9	5	9	4	9
	16	8	8	8	9	7	9	5	9	4	10
	17	8.5	9	9	9	8	9	6	10	4	10
	18	9	9	9	10	8	10	7	10	5	10
	19	9.5	10	10	10	9	10	8	10	5	10

			$L = 0$	$L = 1$		$L = 3$		$L = 5$	
(b)	r_A	m	$n_L = n_U$	n_L	n_U	n_L	n_U	n_L	n_U
	250	50	50	45	55	36	64	29	71
	275	55	55	50	60	40	68	33	75
	300	60	60	55	65	45	72	36	78
	325	65	65	60	69	50	76	41	81
	350	70	70	66	74	55	80	45	84
	375	75	75	71	79	61	84	50	87
	400	80	80	77	83	67	87	55	90
	425	85	85	82	88	73	91	61	93
	450	90	90	88	92	81	94	68	95
	475	95	95	94	96	90	97	78	98

Note: Upper and lower feasible limits n_L and n_U, and input matching distribution m, for a range of values of the total number of animals N, the input rate r_A on site A and the perceptual limit L. (a) Small numbers ($N = 10$, $r_A + r_B = 20$). (b) Large numbers ($N = 100$, $r_A + r_B = 500$).

the intake rate has more effect on the intake per animal on the site with fewer animals. Thus, for large N, we see the range of feasible distributions decreasing (although not smoothly) as r_A increases. However, for small N, rounding and integer effects can result in the range of feasible distributions appearing to oscillate between adjacent values as r_A increases, rather than decreasing monotonically.

For N large and for $r_A = r_B$, the range of feasible distributions is centred on the input matching distribution. Computations indicate that the mid-point of the range then initially decreases *relative to* the corresponding input matching distribution as r_A increases and, finally, increases again towards equality with the input matching distribution as the balance of resources shifts entirely to site A. For small N, the mid-point of the range behaves similarly, but with noticeable exceptions due to integer and rounding effects. Indeed, for small parameter values, the mid-point can sometimes be greater than the corresponding input matching distribution, as shown in Table 2 for the case $L = 0.25$.

Note that, although the running mean of the distributions of animals tends to the true average of the Markov chain, the full range of feasible distributions continues to appear over time. In an experimental context, this would suggest that rather than waiting for distributions of real animals to settle down, repeated counts should be taken or repeated independent trials should be performed. An illustration of random movements over the development of the system and the range of distributions that occur is given in Lang (2000).

Model predictions for the equilibrium probability distribution

Under the Markov chain model, the exact equilibrium probabilities for N_A, the number on site A, are given (see Appendix 2) by

$$P(N_A = n) = p(n) / \sum_{k=n_L}^{n_U} p(k) \qquad n = n_L, \ldots, n_U$$

where $p(n) = N!/[n!(N-n)!2^N]$, $n = 0, \ldots, N$. These equilibrium probabilities are exactly the same as the probabilities for a binomial (N, 1/2) random variable, conditioned to take values in the set $\{n_L, \ldots, n_U\}$. Note that they depend only on the values of N, n_L and n_U, and depend on the parameters L, r_A and r_B only inasmuch as these parameters determine the values of n_L and n_U through equations (2) and (3).

Intuitively, under the operation of the perceptual limit model, each of the N animals repeatedly chooses between sites A and B with equal probability (subject to the constraints of n_L and n_U). When observed at a time point far in the future, each of the N animals is, independently, equally likely to be on A or B, so the total number on site A has a binomial (N, 1/2) distribution.

The equilibrium probability distribution and its expected value inherit several qualitative properties from the binomial distribution. This enables us to more fully understand qualitative features, such as the similarity to the truncated normal distribution, identified in the simulation results of Cartar and Abrahams (1997). These properties include:

(D1) The binomial (N, 1/2) distribution has a standard bell-shape, symmetric about its mid-point at $N/2$. The equilibrium probability distribution has exactly the same shape, except truncated to lie between n_L and n_U. Thus the *relative* values of the $P(N_A = n)$ are exactly the same as the corresponding values for the unrestricted binomial distribution, but their *absolute* values are scaled so that they sum to 1 over the values $n_L, \ldots, n_U$.

(D2) For even moderate values of N, the normal distribution with mean $N/2$ and variance $N/4$ provides a good approximation to the binomial (N, 1/2), so the equilibrium probability distribution is well approximated by a truncated normal distribution.

(D3) The shape of the binomial distribution implies that if the mid-point of n_L and n_U is less than $N/2$ (the mid-point of the binomial (N, 1/2) distribution), then the equilibrium probability distribution and its expected value will be skewed to the right-hand end of the interval (n_L, n_U); if the mid-point is greater than $N/2$, then the equilibrium probability distribution and its expected value will be skewed to the left-hand end of the interval.

(D4) For small n_L and large n_U, the equilibrium probability distribution will be close to the unrestricted binomial (N, 1/2) distribution, and so will be approximately symmetric with an expected value of $N/2$, irrespective of the actual values of L, r_A and r_B.

Table 3 illustrates how variation of the equilibrium probabilities with the perceptual limit L can be related to the qualitative properties (L1–L2) and (D1–D4). The table gives the equilibrium probability of each of the feasible distributions for 10 animals distributing themselves between two sites with input rates of 14 and 6, respectively (parameters used by Abrahams, 1986). As described in the development of the model, when the perceptual limit is zero, only one distribution is usually feasible (the $L = 0$ distribution). As the perceptual limit increases, the range of feasible distributions increases (L1). Since here $r_A > r_B$, the centre of the range is greater than $N/2 = 5$, so the equilibrium probability distribution is proportional to a binomial (5, 1/2) distribution, but over a part of its range where it is skewed to the left (D3). This asymmetrical distribution is consistent with the simulation results of Cartar and Abrahams (1997: fig. 2), and is not simply symmetrical noise around the input matching distribution where there is a small, equal probability of distributions above and below the input matching distribution.

As L increases further, some skewness remains, but as the range of feasible distributions

Table 3. The effect of perceptual limits on equilibrium probabilities

		Perceptual limit				
N_A	N_B	0	0.25	0.50	2.00	3.00
3	7					0.1241
4	6				0.2479	0.2172
5	5				0.2975	0.2606
6	4			0.5600	0.2479	0.2172
7	3	1.0000	0.7273	0.3200	0.1417	0.1241
8	2		0.2727	0.1200	0.0531	0.0465
9	1				0.0118	0.0103
Average number on site A		7.00	7.27	6.56	5.49	5.18

Note: The equilibrium probability of each of the feasible distributions of animals between two sites, together with the average number on site A, for a range of perceptual limits (L). Parameters used are $N = 10$, $r_A = 14$, $r_B = 6$.

increases towards the full range of the binomial (5, 1/2) distribution, the equilibrium probability distribution itself becomes more like the binomial (5, 1/2) distribution, which is symmetric about $N/2 = 5$.

In the example in Table 3, input matching predicts 7 animals on site A. We can see that for $L = 0.25$, the feasible distributions are 7 and 8 animals on site A, and the expected number on site A is greater than the input matching distribution. However, for $L = 0.5$, the feasible distributions are 6, 7 and 8 animals on site A, and the distribution is skewed to the lower end of the range, so the expected number on site A is less than that predicted by input matching. Thus, especially when there are integer and rounding effects, the perceptual limit model can predict both the overuse and the underuse of the best site, termed over-matching and under-matching, respectively (Kennedy and Gray, 1993).

Model predictions for the expected number on each site

For large N, the qualitative behaviour of the expected number on site A can often be inferred from the properties (L1–L2) and (D1–D4). For example, as r_A increases with $r_A + r_B$ fixed, both ends of the feasible range (and hence its mid-point) initially increase (L2), so the probability distribution becomes more skewed to the left (D3) and the mean decreases relative to the mid-point. The mid-point itself is less than the input matching distribution, so the mean is also less than the input matching distribution, and this difference increases with r_A as the skewness increases and the difference between the mid-point and the input matching distribution increases. However, as r_A increases further, the range of feasible values decreases and the difference between the mid-point and the input matching distribution decreases, so the mean now becomes closer to the mid-point and hence to the input matching distribution. Similarly, for fixed r_A, the difference between the mean and the input matching distribution increases with L (L1).

Figure 1b illustrates these points, using parameter values of $N = 100$ and $r_A + r_B = 500$, for comparison with the example of Cartar and Abrahams (1997). Note that, when the input rates at the two sites are equal, the $L = 0$ distribution and the expected value of the equilibrium distribution coincide and so there is no effect of perceptual limit on the average number on each site, although of course the variance increases with L because the range of feasible distributions increases. When all resources are on site A, the difference in intake rates at the two sites is much greater than the highest perceptual limit used and so there are no random movements. Between these two extremes, the divergence of the expected value from the $L = 0$ distribution and/or the input matching distribution first increases then decreases as explained above.

When N is small, the predictions above are often outweighed by integer and rounding effects. Figure 1a illustrates this, with a plot of the expected number on site A predicted by the model for a constant number of animals ($N = 10$) under a range of perceptual limits. The parameter values used were chosen for comparability with Abrahams (1986). We have not extended the values through the y-axis by swapping the sites (i.e. taking the value of r_A below 10) as in Abrahams (1986), because this provides no additional information. Again, when there is no perceptual limit, increasing the input rate on site A increases the number of animals on this site. The figure shows that divergence from the $L = 0$ distribution increases as the asymmetry of the input rates increase. These results are in line with those of Abrahams (1986) and Cartar and Abrahams (1997) using simulations.

Model predictions for the average intake rate on each site

Whatever the probability distribution for the number on site A, the overall expected intake rate for a randomly chosen animal is exactly equal to $(r_A + r_B)/N$. This is the same as the rate achieved under the input matching distribution, even though there will usually be no feasible distribution of animals that results in input matching.

However, the feasibility of distributions other than input matching is of significance when the intake rate of individual animals is considered. At input matching, each animal achieves the same intake rate, irrespective of the site. For distributions other than input matching, there will be asymmetries in the intake rates achieved by animals on the two sites. Thus, the variability of the intake rate for a randomly chosen animal increases as the range of feasible distributions increases, and there may be significant variability between the expected intake on different sites and between the expected total intake of different animals.

We look first at the average intake rate on each site. Figure 2 shows the expected intake rates achieved by animals on each site, for parameter values similar to those used by Abrahams (1986) and Cartar and Abrahams (1997). Interestingly, even when $L = 0$, the inability of the animals to distribute according to input matching can lead to asymmetries in intake rates. In this example when $L = 0$, $r_A = 17$ and $r_B = 3$, the average intake on site B is 3 compared to 1.89 on site A. As described above, increasing the perceptual limit increases the divergence from input matching. Figure 2a shows that this leads to increased asymmetries in the average intake rates at the two sites.

When N is large, as in Fig. 2b, the integer effects are greatly reduced. Although the exact expected values are plotted, the expected intake rate on each site is approximately equal to r_A divided by the expected number on that site. Thus, the expected intake rate achieved on site A now diverges from the $L = 0$ condition in a curve that has the maximum divergence when the expected number on site A is also at its maximum divergence from the $L = 0$ condition (Fig. 2b). However, the expected intake rate on site B continues to decrease with increasing input rate asymmetry.

Note also that intake rates observed in individual trials may differ more than the illustrations in Fig. 2 because of the random variation of distributions around each average.

Model predictions for individual intake rates

The Markov chain model can be extended to derive the joint equilibrium distribution of the number of animals on site A and the site occupied by a given focal animal (Appendix 3). Using this equilibrium distribution, it can be shown that the long-term average intake per unit time of each single focal animal is exactly equal to the value $(r_A + r_B)/N$, which would be predicted by the ‘input matching rule’ of Parker (1978), irrespective of its initial state and even in cases where there is no feasible distribution that results in the input matching distribution.

However, there are significant differences in the expected total intake of individual animals and in the variability of their total intake, depending on their initial state. In particular, over the medium term, computations indicate that an animal normally does better on average if it starts on the site with higher input rate, even when the initial number on that site is at the upper end of the range of feasible distributions and a comparison of intake rates over a single time period would favour the alternative site.

To see why this might be so, consider the case when $r_A > r_B$ and $n_L > N/2$. The range of

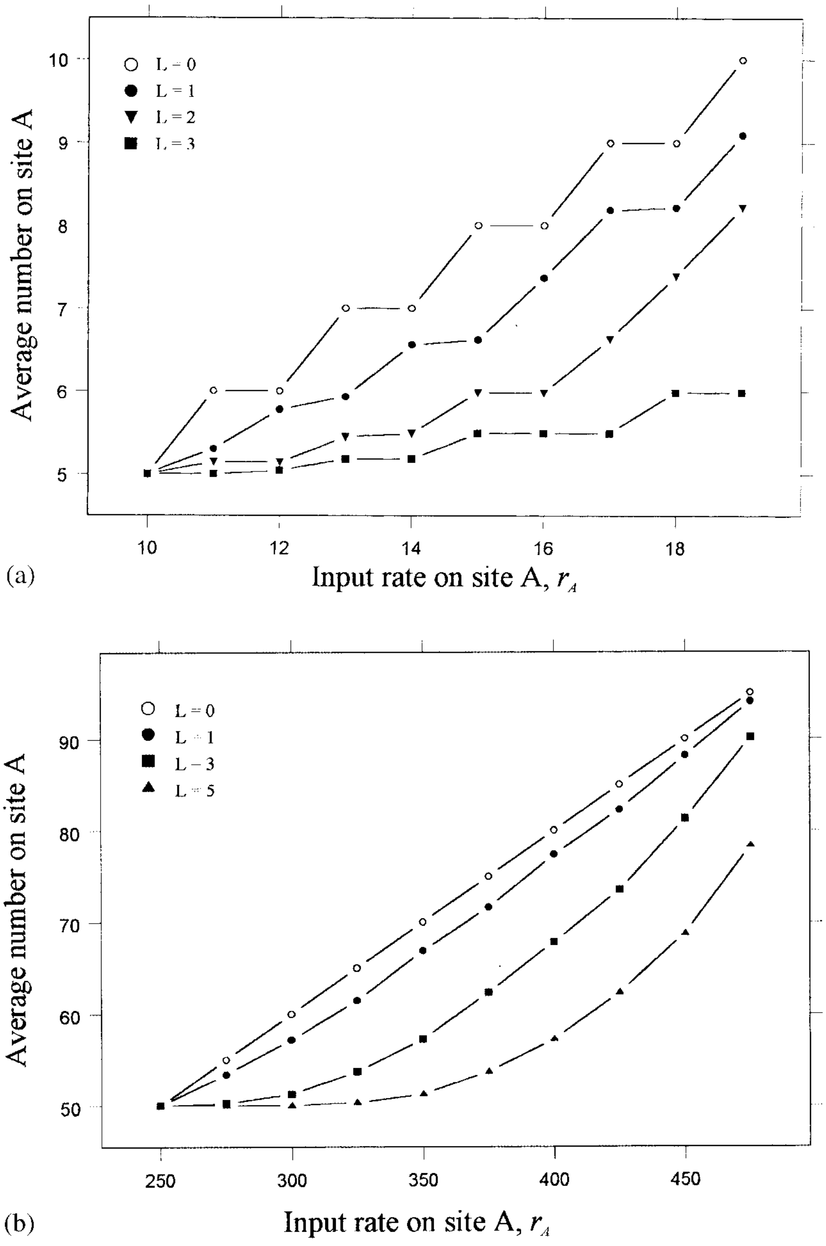

Fig. 1. The average distribution of animals is given for four values of perceptual limit (L). The total input rate is fixed and the proportion on each site is varied. (a) Small numbers: $r_A + r_B = 20$, $N = 10$. (b) Large numbers: $N = 100$, $r_A + r_B = 500$.

feasible distributions then ensures that there will always be more animals on site A than site B. Since an animal is chosen at random at each time point, it is more likely that the potentially moving animal will be chosen from site A, so – where possible – movements

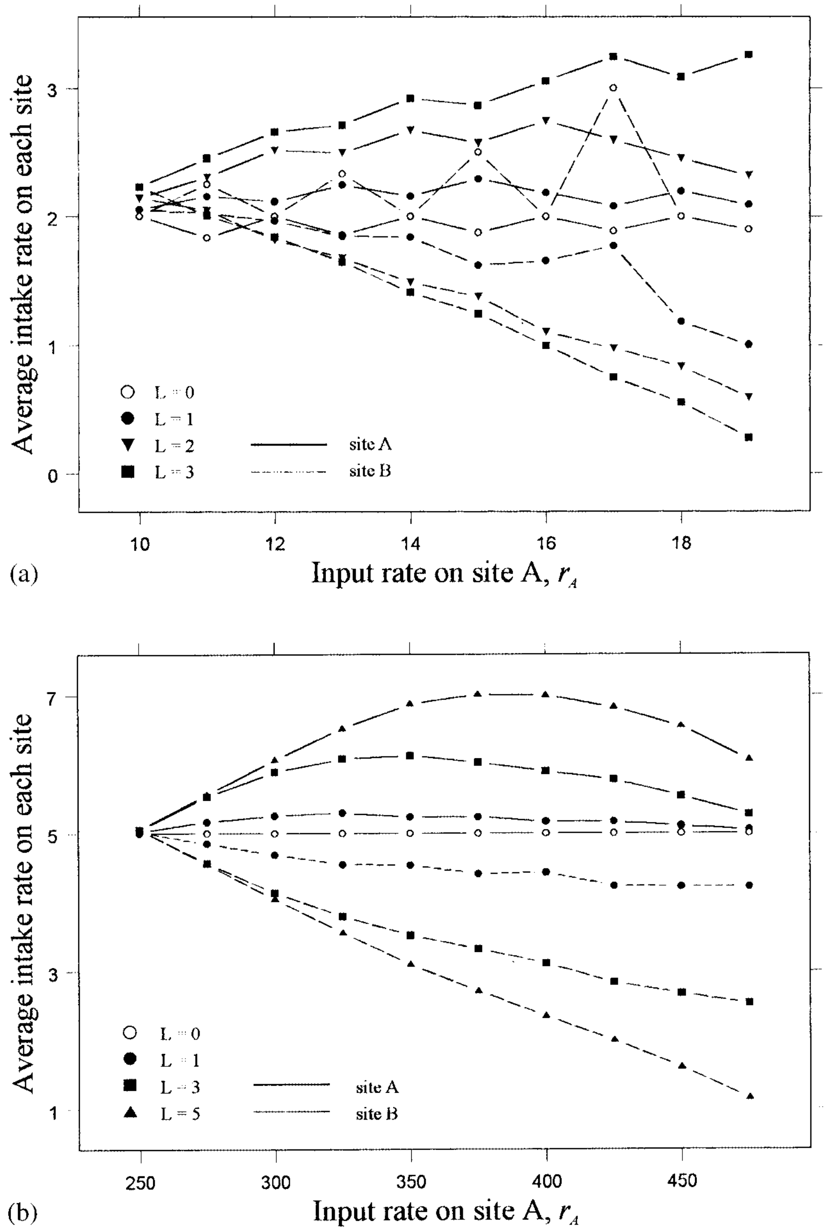

Fig. 2. The intake rate for the average distribution is shown for four values of perceptual limit (L). (a) Small numbers ($r_A + r_B = 20$, $N = 10$). (b) Large numbers ($N = 100$, $r_A + r_B = 500$). Solid lines are for animals on site A and dashed lines for animals on site B. Note that for $L = 0$, there is no difference in intake rates between the two locations.

resulting in lower values of the number on site A are more likely. Moreover, since $r_A > r_B$, each unit increase in the number on site B has a greater effect on the intake rate per animal on that site than that of a similar increase on site A.

For a more concrete example, consider computing the expected total intake over two time periods when the parameter values are such that $r_A > r_B$ and $Nr_A/(r_A + r_B)$ takes an integer value, say m. Then, $r_A/m = r_B/(N - m)$, and m corresponds to the input matching distribution on site A. Consider the case where two focal animals start at time point $t = 0$, one on site A and one on site B, with an initial distribution of m animals on site A and $N - m$ animals on site B. The choice of m as the input matching distribution ensures that, over the first time period, the intakes of both animals will have exactly the same value, r_A/Nm, and in this sense both sites are equally attractive. However, the expected total intake over two time periods for the animal that starts on site A exceeds that for the animal that starts on site B by an amount $(r_A - r_B)/[2(m + 1)(N - m + 1)] > 0$ (see Appendix 3). Thus, even looking just two time steps ahead, there is a trade-off between the intake in the current state and the probability of moving to a state with a high intake over the next time period. The immediate intake rate is not on its own a good predictor of total intake over the two periods and, in that sense, an animal would be better off starting on the site with larger input rate.

Figure 3 plots the difference between the expected total long-term intake that the focal animal would receive under the perceptual limit model and the corresponding total intake if its intake was exactly $(r_A + r_B)/N$ per time unit (as would result from input matching). The plots show the differences for a range of parameter values and for four different initial states. Note that the values of n_L and n_U will vary with the parameters selected. As one would expect, the animal does better starting on A when there are fewer other animals on A than when there are more. What is perhaps more surprising is that the animal does better starting on A when the number on A is at its maximum, than it would if it started on B when the number on A was at its maximum and the number on B was at its minimum.

An alternative way of quantifying the effect of initial state is in terms of the resulting variability in the total intake for the focal animal, say over a fixed time T. Although the intakes in successive time periods are not independent, a recursion formula for computing this variance can easily be derived (see Appendix 3).

Identifying perceptual limits

Gray and Kennedy (1994) conducted feeding trials with mallard ducks (*Anas platyrhynchos*) and calculated the average distribution of ducks between two patches. Using a simulation model, they estimated the perceptual limit that would give rise to the deviation of the observed average from that predicted by input matching. However, there could be other reasons for the deviation of the average value. If observed distributions of animals between patches differ from input matching in a way that can be modelled by the perceptual limit model, then we should get a good estimate of the perceptual limit from the range of observed distributions.

Consider the equilibrium probabilities calculated using the model for $L = 2.0$ in Table 3. We know that the minimum feasible distribution of the perceptual limit model (in terms of number of animals on site A) occurs when no animal moves at random from site A to site B (i.e. $G_{AB} > -L$). For this example, the observed minimum is 4 and thus we know from Table 1 that $L < 2.64$. At the minimum, an animal will, however, move from site B to site A (i.e. $G_{BA} \leq L$) and so $L \geq 1.8$. Similarly, the maximum feasible distribution occurs when no animal moves at random from site B to site A, but an animal will move at random in the opposite direction. Given the observed maximum of 9 animals on A, we get a second estimate of $1.44 < L \leq 4.6$. From the overlap of these two estimates, we get $1.8 \leq L < 2.64$,

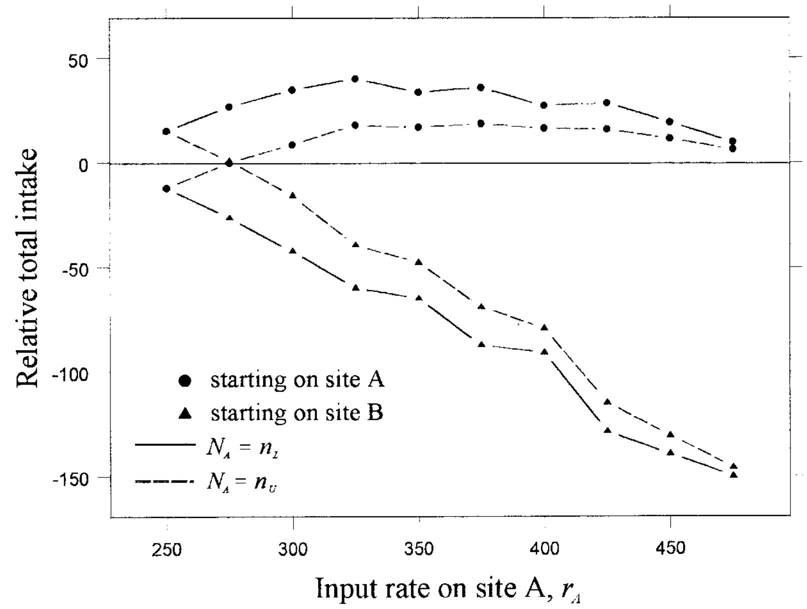

Fig. 3. The relative total intake (i.e. the difference between the expected total long-term intake an animal would receive under the perceptual limit model and the corresponding total under input matching) for four different initial states: (a) the number on site A is at its minimum feasible value and the focal animal starts on site A; (b) the number on site A is at its maximum feasible value and the focal animal starts on site A; (c) the number on site A is at its minimum feasible value and the focal animal starts on site B; and (d) the number on site A is at its maximum feasible value and the focal animal starts on site B. The perceptual limit and the total input rate are fixed ($N = 100$, $L = 1$, $r_A + r_B = 500$) and the proportion on each site is varied.

which includes the true value of $L = 2$. For comparison, consider the fictional equilibrium probabilities $P(4) = 0.21$, $P(5) = 0.29$, $P(6) = 0.30$, $P(7) = 0.20$ with the same average (5.49) as that calculated for $L = 0.5$ in Table 3. The minimum fictional feasible distribution is 4 and thus one estimate of L coincides with that for the perceptual limit model. However, the observed maximum fictional feasible distribution is 7, which gives a second estimate of $0.25 \leq L < 0.50$. Thus the two estimates of the perceptual limit from the fictional equilibrium probabilities are not consistent and cannot have been caused by a constant perceptual limit as modelled here. We would suggest, therefore, that simply comparing observed and predicted average distributions can lead to misleading conclusions.

DISCUSSION

We have presented a new method for analysing the model of Abrahams (1986) for identical animals with a perceptual limit distributing themselves between two sites. The Markov chain model we developed allows us to find an exact expression for the equilibrium probability of each feasible distribution of animals. For each set of parameters, the range of feasible distributions is determined by the limits on random movements. These limits can be calculated by simple quadratic equations. In contrast to analyses of animals switching between sites that predict a distribution between input matching and equal numbers (Houston *et al.*, 1995), feasible distributions include underuse and overuse of the best site. Although the model can be used to predict the expected number of animals on a site, there is typically a range of possible outcomes that will continue to be observed over time in any experimental or simulated realization of the system. Furthermore, even with a zero perceptual limit we observe unequal intake rates when the number of animals cannot divide between the available sites according to input matching. These two points are important when analysing feeding experiments. Clearly, using small numbers of animals may lead to integer effects. Also, there is no single distribution for animals when there is a perceptual limit and, therefore, repeated sampling of observed distributions is necessary to provide information on the range the distributions that can occur.

The lack of a single stable distribution for the perceptual limit model highlights an important difference between this model and the basic ideal free distribution model. In the basic model, animals have no reason to switch after arrival. In the perceptual limit model, switching continues after arrival. The statement by Spencer *et al.* (1995) that 'The distribution of organisms did not stabilize until well after all the individuals had arrived in the system' is potentially misleading in this respect. Although we can calculate the equilibrium probability of each feasible distribution and can calculate an average, the observed distribution will not tend to this average distribution. Rather, all feasible distributions will continue to occur.

The observed range of feasible distributions can be used to estimate the perceptual limit that would cause this range. It should be noted that, as Spencer *et al.* (1996) pointed out, a perceptual limit is not likely to be the threshold limit assumed in the perceptual limit model. Instead of the animal moving with probability 1 or 0.5, the probability of an animal identifying one potential intake rate as being larger than another is likely to be a continuous function of the difference between the two rates (cf. Houston *et al.*, 1995). However, consistent estimates of the perceptual limit calculated from the observed distributions would provide empirical support for the perceptual limit model.

Currently, support for the model is drawn from two facts. First, the perceptual limit model predicts the type of underuse of the best site observed in feeding trials (Gray and Kennedy, 1994). Secondly, the perceptual limit model predicts that reducing the overall level of resource in the environment will increase the extent of underuse of the best site (Abrahams, 1986), which has been observed in feeding trials (Gray and Kennedy, 1994). However, analyses of animals distributing themselves between two sites using a variety of learning and decision rules also found underuse of the best site that increased with reduced input rates (Lang, 2000). Therefore, more specific empirical support for the perceptual limit model is clearly necessary.

A novel feature of our analysis is the investigation of the effect of the site that an individual chooses on the individual's expected total intake. Our computations indicate that, over the medium term, an animal typically has a higher intake if it starts on the site with the higher input rate, even when the current number of animals on that site is at the upper end of the range of feasible distributions and the intake rate over a single decision period would be higher on the alternative site. In particular, we have shown that maximizing the immediate intake rate may not result in the highest total intake over two periods. Many models of ideal free distributions are based on the assumption that each animal goes to the site that currently offers it the highest rate of gain. Our demonstration that such a rule does not maximize total gain suggests that a full understanding of the evolutionary stability of rules for choosing between sites must go beyond immediate maximization (cf. Houston and Lang, 1998: 249). The generality of the effect of initial site chosen on total intake for other models of switching deserves investigation.

Several authors have used log–log plots for analysing ideal free distributions, based on the assumption that the overall distribution of animals can be modelled more precisely by the equation $N_A/N_B = a(r_A/r_B)^s$ than by input matching. Taking logs of both sides gives $\log(N_A/N_B) = \log a + s\log(r_A/r_B)$ and so a and s can be estimated from the slope and the intercept of the log–log plot, respectively. Let $\bar{N}_A$ and $\bar{N}_B$ denote the average number of animals predicted on site A and site B, respectively, by the perceptual limit model. Although the model does not lead to simple expressions for $\bar{N}_A/\bar{N}_B$ as a function of r_A/r_B, the relationship between them is certainly non-linear, as is that between $\log(\bar{N}_A/\bar{N}_B)$ and $\log(r_A/r_B)$. For small numbers of animals, this non-linearity may not be immediately obvious in log–log plots of the predicted values of $\log(\bar{N}_A/\bar{N}_B)$ against $\log(r_A/r_B)$. However, for large numbers of animals, the plots are clearly non-linear and the deviation from linearity increases with increasing L (Lang, 2000). Thus the perceptual limit provides no support for an overall relationship of the form $N_A/N_B = a(r_A/r_B)^s$.

In principle, the Markov chain model can be extended to the case of unequal competitors and to the case of more than two sites. However, in each case, the set of long-term feasible distributions can have a more complicated structure than for the two-site equal-competitors case discussed above, especially when the number of animals or the perceptual limit is small. Although the equilibrium probability distribution can still be computed numerically, prediction and inference from the results can be much less clear.

For the case of unequal competitors with two classes of fixed competitive weights, the proportion of food available at a location that an animal will gain is given by the animal's competitive ability divided by the total competitive ability of all animals at that location (Sutherland and Parker, 1985; Parker and Sutherland, 1986). In contrast to the basic ideal free distribution, there are usually several possible solutions to distributions of unequal competitors (Sutherland and Parker, 1985; Parker and Sutherland, 1986; Houston and McNamara, 1988) and the method of modelling the distribution can affect the predicted outcomes (Spencer *et al.*, 1995, 1996; Houston and Lang, 1998). When we look at this model in the context of a perceptual limit, the problem is that the set of feasible distributions may split into several distinct subsets, of which only one will appear long-term in any particular simulation or experiment. However, the subset that does appear may depend in a possibly random way on the initial conditions or early movements of the system. This has important implications for the interpretation of experimental results.

For the case of N animals distributed over $K > 2$ sites, with input rates $r_1, \ldots, r_K$, one can easily show that, for large L, the equilibrium probability distribution for the Markov chain is a multinomial distribution. In this case, the probability of observing $n_1, \ldots, n_K$ animals on the respective sites has the form $N!/(n_1!n_2! \ldots n_K!\, K^N)$, irrespective of the values of $r_1, \ldots, r_K$, and the mean number on each site is N/K, consistent with the observation of Cartar and Abrahams (1997). Unfortunately, for smaller values of L, the Markov chain model will usually not be reversible and, unlike the two-site case, the equilibrium probability distribution will no longer be a simple truncation of the distribution for large L given above.

ACKNOWLEDGEMENTS

A.L. was supported by a studentship that formed part of a NERC Special Topics Project (Principal Investigator John Goss-Custard, GT24/95/LSPE/4). We thank Tom Caraco for comments on a previous draft of the manuscript.

REFERENCES

Abrahams, M.V. 1986. Patch choice under perceptual constraints: a cause for departure from an ideal free distribution. *Behav. Ecol. Sociobiol.*, **19**: 409–415.

Baum, W.M. 1974. On two types of deviation from the matching law: bias and undermatching. *J. Exp. Anal. Behav.*, **22**: 231–242.

Baum, W.M. 1979. Matching, undermatching, and overmatching in studies of choice. *J. Exp. Anal. Behav.*, **32**: 269–281.

Cartar, R.V. and Abrahams, M.V. 1997. Predicting the distribution of organisms among a few patches: problems with detecting departures from the ideal free distribution. *Oikos*, **78**: 388–393.

Fretwell, S.D. 1972. *Populations in a Seasonal Environment*. Princeton, NJ: Princeton University Press.

Fretwell, S.D. and Lucas, H.L. 1970. On territorial behaviour and other factors influencing habitat distributions in birds. *Acta Biotheor.*, **19**: 16–36.

Giraldeau, L.-A. and Caraco, T. 2000. *Social Foraging Theory*. Princeton, NJ: Princeton University Press.

Godin, J.-G.J. and Keenleyside, M.H.A. 1984. Foraging on patchily distributed prey by a cichlid fish (Teleosti, Cichlidae): a test of the ideal free distribution theory. *Anim. Behav.*, **32**: 120–131.

Gray, R.D. and Kennedy, M. 1994. Perceptual constraints on optimal foraging: a reason for departures from the ideal free distribution? *Anim. Behav.*, **47**: 469–471.

Harper, D.G.C. 1982. Competitive foraging in mallards: 'ideal free' ducks. *Anim. Behav.*, **30**: 575–584.

Herrnstein, R.J. 1970. On the law of effect. *J. Exp. Anal. Behav.*, **13**: 243–266.

Houston, A.I. and Lang, A. 1998. The ideal free distribution with unequal competitors: the effects of modelling methods. *Anim. Behav.*, **56**: 243–251.

Houston, A.I. and McNamara, J.M. 1988. The ideal free distribution when competitive abilities differ: an approach based on statistical mechanics. *Anim. Behav.*, **36**: 166–174.

Houston, A.I., McNamara, J.M and Milinski, M. 1995. The distribution of animals between resources: a compromise between equal numbers and equal intake rates. *Anim. Behav.*, **49**: 248–251.

Kennedy, M. and Gray, R.D. 1993. Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the ideal free distribution. *Oikos*, **68**: 158–166.

Lang, A. 2000. Individual behaviour and population ecology: developing an individual based model for the Svalbard population of barnacle geese. Doctoral dissertation, University of Bristol.

Milinski, M. 1979. An evolutionary stable feeding strategy in sticklebacks. *Z. Tierpsych.*, **51**: 36–40.

Milinski, M. 1984. Competitive resource sharing: an experimental test of a learning rule for ESS. *Anim. Behav.*, **32**: 233–242.

Milinski, M. and Parker, G.A. 1991. Competing for resources. In *Behavioural Ecology: An Evolutionary Approach* (J.R. Krebs and N.B. Davies, eds), pp. 137–168. Oxford: Blackwell.

Parker, G.A. 1978. Searching for mates. In *Behavioural Ecology: An Evolutionary Approach* (J.R. Krebs and N.B. Davies, eds), pp. 214–244. Oxford: Blackwell.

Parker, G.A. and Sutherland, W.J. 1986. Ideal free distributions when individuals differ in competitive ability. *Anim. Behav.*, **34**: 1222–1242.

Spencer, H.G., Kennedy, M. and Gray, R.D. 1995. Patch choice with competitive asymmetries and perceptual limits: the importance of history. *Anim. Behav.*, **50**: 497–508.

Spencer, H.G., Kennedy, M. and Gray, R.D. 1996. Perceptual constraints on optimal foraging: the effects of variation among foragers. *Evol. Ecol.*, **10**: 331–339.

Sutherland, W.J. and Parker, G.A. 1985. The distribution of unequal competitors. In *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (R.M. Sibly and R.H. Smith, eds), pp. 255–274. Oxford: Blackwell.

Tijms, H.C. 1986. *Stochastic Modelling: A Computational Approach*. Chichester: Wiley.

Tregenza, T. 1995. Building on the ideal free distribution. *Adv. Ecol. Res.*, **26**: 253–307.

APPENDIX 1

Set $G_{\mathrm{AB}}(x) = r_{\mathrm{B}}/(N - x + 1) - r_{\mathrm{A}}/x$ and $G_{\mathrm{BA}}(x) = r_{\mathrm{A}}/(x + 1) - r_{\mathrm{B}}/(N - x)$. Let $\underline{x}_{\mathrm{A}}$ and $\bar{x}_{\mathrm{A}}$ be the values of x for which $G_{\mathrm{AB}}(x) = -L$ and $G_{\mathrm{AB}}(x) = L$, respectively, and let $\bar{x}_{\mathrm{B}}$ and $\underline{x}_{\mathrm{B}}$ be the corresponding values of x for which $G_{\mathrm{BA}}(x) = -L$ and $G_{\mathrm{BA}}(x) = L$. Thus $\underline{x}_{\mathrm{A}}$ is the smaller root of the quadratic equation $x^2L - x(r_{\mathrm{A}} + r_{\mathrm{B}} + L(1 + N)) + r_{\mathrm{A}}\,(N + 1) = 0$, and $\bar{x}_{\mathrm{B}}$ is the larger root of the quadratic equation $x^2L + x(r_{\mathrm{A}} + r_{\mathrm{B}} + L(1 - N)) + r_{\mathrm{B}} - N(r_{\mathrm{A}} + L) = 0$. Note that $G_{\mathrm{AB}}(x) = -G_{\mathrm{BA}}(x - 1)$, so that $\underline{x}_{\mathrm{A}} = \underline{x}_{\mathrm{B}} + 1$ and $\bar{x}_{\mathrm{A}} = \bar{x}_{\mathrm{B}} + 1$, and that for some parameter values $\underline{x}_{\mathrm{A}} > \bar{x}_{\mathrm{B}}$.

Assume now that there are n animals on site A. Under the perceptual limit model, an animal on site A will stay on site A if $G_{\mathrm{AB}}\,(n) < -L$, will move at random if $-L \leq G_{\mathrm{AB}}\,(n) \leq L$ and will move to site B if $G_{\mathrm{AB}}\,(n) > L$. Since $G_{\mathrm{AB}}(x)$ is increasing in x, this means an animal on site A will stay on site A if $n < \underline{x}_{\mathrm{A}}$, will move at random if $\underline{x}_{\mathrm{A}} \leq n \leq \bar{x}_{\mathrm{A}}$ and will move to site B if $n > \bar{x}_{\mathrm{A}}$. Using a similar argument and the fact that $G_{\mathrm{BA}}(x)$ is decreasing in x, we see that an animal on site B will stay on site B if $n > \bar{x}_{\mathrm{B}}$, will move at random if $\underline{x}_{\mathrm{B}} \leq n \leq \bar{x}_{\mathrm{B}}$ and will move to site A if $n < \underline{x}_{\mathrm{B}}$, where $\bar{x}_{\mathrm{B}} = \bar{x}_{\mathrm{A}} - 1$ and $\underline{x}_{\mathrm{B}} = \underline{x}_{\mathrm{A}} - 1$.

The limits of the feasible distributions can now be calculated from these limits on random movements. For values of n with $\underline{x}_{\mathrm{A}} \leq n \leq \bar{x}_{\mathrm{B}}$, animals on both site A and site B will move at random, so values of n with $\underline{x}_{\mathrm{A}} - 1 \leq n \leq \bar{x}_{\mathrm{B}} + 1$ are attainable. For $\underline{x}_{\mathrm{B}} = \underline{x}_{\mathrm{A}} - 1 \leq n < \underline{x}_{\mathrm{A}}$, animals on site A will not move to site B (although animals on site B are prepared to move to site A), so n cannot decrease. For $\bar{x}_{\mathrm{B}} = \bar{x}_{\mathrm{A}} - 1 < n \leq \bar{x}_{\mathrm{A}}$, animals on site B will not move to site A (although animals on site A are prepared to move to site B), so n cannot increase. Thus the lower minimum number n_{L} on site A is given by the next integer below $\underline{x}_{\mathrm{A}}$, and the upper maximum number n_{U} is given by the next integer above $\bar{x}_{\mathrm{B}}$.

APPENDIX 2

States and transition probabilities

Let $N_{\mathrm{A}}(t)$ denote the number of animals on site A at time t, starting at some time, say $t = 0$, when all N animals are present on the two sites. Let n_{L} and n_{U} be the limits on the feasible distributions calculated from the appropriate roots of equations (2) and (3).

Under the perceptual limit model, an animal is chosen at random from the population at each time point; if the animal is currently on site A, then under the model it will stay on site A if $N_{\mathrm{A}}(t) \leq n_{\mathrm{L}}$ and will switch to B if $N_{\mathrm{A}}(t) > n_{\mathrm{U}}$; if the animal is currently on site B, then it will switch to A if $N_{\mathrm{A}}(t) < n_{\mathrm{L}}$ and will stay on B if $N_{\mathrm{A}}(t) \geq n_{\mathrm{U}}$; in all other cases, the animal will randomize with equal probability between staying on the current site and switching sites.

Straightforward computation shows that $\{N_{\mathrm{A}}(t)\colon t = 0, 1, 2, \ldots\}$ is a Markov chain with state space $\{0, 1, \ldots, N\}$ and stationary transition probabilities:

$$\left.\begin{aligned} &P(N_{\mathrm{A}}(t+1)=n \mid N_{\mathrm{A}}(t)=n)=n/N \\ &P(N_{\mathrm{A}}(t+1)=n+1 \mid N_{\mathrm{A}}(t)=n)=(N-n)/N \end{aligned}\right\} n=0,\ldots,n_{\mathrm{L}}-1$$

$$\left.\begin{aligned} &P(N_{\mathrm{A}}(t+1)=n \mid N_{\mathrm{A}}(t)=n)=n/N+(N-n)/2N \\ &P(N_{\mathrm{A}}(t+1)=n+1 \mid N_{\mathrm{A}}(t)=n)=(N-n)/2N \end{aligned}\right\} n=n_{\mathrm{L}}$$

$$\left.\begin{aligned} &P(N_{\mathrm{A}}(t+1)=n-1 \mid N_{\mathrm{A}}(t)=n)=n/2N \\ &P(N_{\mathrm{A}}(t+1)=n \mid N_{\mathrm{A}}(t)=n)=1/2 \\ &P(N_{\mathrm{A}}(t+1)=n+1 \mid N_{\mathrm{A}}(t)=n)=(N-n)/2N \end{aligned}\right\} n=n_{\mathrm{L}}+1,\ldots,n_{\mathrm{U}}-1$$

$$\left.\begin{aligned} &P(N_{\mathrm{A}}(t+1)=n-1 \mid N_{\mathrm{A}}(t)=n)=n/2N \\ &P(N_{\mathrm{A}}(t+1)=n \mid N_{\mathrm{A}}(t)=n)=(N-n)/N+n/2N \end{aligned}\right\} n=n_{\mathrm{U}}$$

$$\left.\begin{aligned} &P(N_{\mathrm{A}}(t+1)=n-1 \mid N_{\mathrm{A}}(t)=n)=n/N \\ &P(N_{\mathrm{A}}(t+1)=n \mid N_{\mathrm{A}}(t)=n)=(N-n)/N \end{aligned}\right\} n=n_{\mathrm{U}}+1,\ldots,N$$

Equilibrium probability distribution

Clearly the set $\{n_{\mathrm{L}},\ldots,n_{\mathrm{U}}\}$ forms a single irreducible class of aperiodic persistent states, while the remaining states are transient. The limiting or equilibrium behaviour of the chain is, therefore, the same as that of a modified chain with the same transition probabilities but with restricted state space $\{n_{\mathrm{L}},\ldots,n_{\mathrm{U}}\}$. The equilibrium probabilities for this modified chain are the unique positive numbers $\pi_n = P(N_{\mathrm{A}}=n)$, $n=n_{\mathrm{L}},\ldots,n_{\mathrm{U}}$ satisfying the normalization equation

$$\sum_{n=n_{\mathrm{L}}}^{n_{\mathrm{U}}} \pi_n = 1 \tag{A1}$$

and the full balance equations

$$\left.\begin{array}{ll} \pi_n=\pi_n(n/N+(N-n)/2N)+\pi_{n+1}(n+1)/2N & n=n_{\mathrm{L}} \\ \pi_n=\pi_{n-1}(N-n+1)/2N+\pi_n/2+\pi_n(n+1)/2N & n=n_{\mathrm{L}}+1,\ldots,n_{\mathrm{U}}-1 \\ \pi_n=\pi_{n-1}(N-n+1)/2N+\pi_n((N-n)/N+n/2N) & n=n_{\mathrm{U}} \end{array}\right\} \tag{A2}$$

Since the modified chain is, in fact, reversible, the π_n can be obtained more simply from the detailed balance equations

$$\pi_n(N-n)/2N=\pi_{n+1}(n+1)/2N \qquad n=n_{\mathrm{L}},\ldots,n_{\mathrm{U}} \tag{A3}$$

which have solution

$$\pi_n \propto \frac{1}{n!(N-n)!} \qquad n=n_{\mathrm{L}},\ldots,n_{\mathrm{U}} \tag{A4}$$

Now set

$$p(n)=\binom{N}{n}\frac{1}{2^N}=\frac{N!}{n!(N-n)!\,2^N} \qquad n=0,\ldots,N \tag{A5}$$

Since the constant of proportionality in (A4) is determined by the normalization equation (A1), an exact explicit expression for the π_n is given by

$$\pi_n=p(n)\Big/\sum_{k=n_{\mathrm{L}}}^{n_{\mathrm{U}}} p(k) \qquad n=n_{\mathrm{L}},\ldots,n_{\mathrm{U}} \tag{A6}$$

and an exact explicit expression for the corresponding mean of the equilibrium distribution is given by

$$E(N_{\mathrm{A}}) = \sum\nolimits_{n=n_{\mathrm{L}}}^{n_{\mathrm{U}}} np(n) / \sum\nolimits_{n=n_{\mathrm{L}}}^{n_{\mathrm{U}}} p(n) \tag{A7}$$

Insight into the equilibrium distribution is obtained by considering a random variable X with binomial (N, 1/2) distribution. The probability distribution of X is then

$$P(X = n) = \binom{N}{n}\frac{1}{2^N} = p(n) \qquad\qquad n = 0, \ldots, N$$

Furthermore, for $n = n_{\mathrm{L}}, \ldots, n_{\mathrm{U}}$, the conditional probabilities $P(X = n \mid n_{\mathrm{L}} \le X \le n_{\mathrm{U}})$ have the form $P(X = n \mid n_{\mathrm{L}} \le X \le n_{\mathrm{U}}) = p(n)/\sum\nolimits_{k=n_{\mathrm{L}}}^{n_{\mathrm{U}}} p(k)$. Thus the equilibrium probabilities for the chain are exactly those for a binomial (N, 1/2) random variable, conditioned to take values in the set $\{n_{\mathrm{L}}, \ldots, n_{\mathrm{U}}\}$.

Expected value and variance of the number on each site in equilibrium

The expected value of N_{A} (and that of $r_{\mathrm{A}}/N_{\mathrm{A}}$ and $r_{\mathrm{B}}/(N - N_{\mathrm{A}})$) can easily be obtained directly for N small or, using the recursion (A3), for N large. The expected value of N^2_{A}, and hence the variance of N_{A}, can be computed similarly. The expected value of the number N_{B} on site B is then given by $E(N_{\mathrm{B}}) = N - E(N_{\mathrm{A}})$, and its variance is exactly the same as that of N_{A}.

Alternatively, for moderate values of N, the normal distribution with mean $N/2$ and variance $N/4$ provides an excellent approximation to the binomial (N, 1/2) distribution. Using appropriate continuity corrections, this approximation gives

$$\begin{aligned}
&E(N_{\mathrm{A}}) = N/2 - \sqrt{N/4}\,(\phi(z_{\mathrm{U}}) - \phi(z_{\mathrm{L}}))/(\Phi(z_{\mathrm{U}}) - \Phi(z_{\mathrm{L}}))\\
&V(N_{\mathrm{A}}) = N/4 - N/4\,[((z_{\mathrm{U}}\phi(z_{\mathrm{U}}) - z_{\mathrm{L}}\phi(z_{\mathrm{L}}))/(\Phi(z_{\mathrm{U}}) - \Phi(z_{\mathrm{L}}))) + ((\phi(z_{\mathrm{L}}) - \phi(z_{\mathrm{U}}))/(\Phi(z_{\mathrm{U}}) - \Phi(z_{\mathrm{L}})))^2]
\end{aligned}$$

where $z_{\mathrm{L}} = (n_{\mathrm{L}} - N/2 - 1/2)/\sqrt{N/4}$ and $z_{\mathrm{U}} = (n_{\mathrm{U}} - N/2 + 1/2)/\sqrt{N/4}$, and where $\phi(\cdot)$ and $\Phi(\cdot)$ respectively denote the probability density function and the cumulative distribution function for the standard normal $N(0, 1)$ distribution. Note that for very large values of n_{L}, the distribution is heavily skewed to the left (D3), and we have the further simplification that $E(N_{\mathrm{A}}) \cong n_{\mathrm{L}}$.

APPENDIX 3

States and transition probabilities

Let $X(t)$ denote the state of the extended Markov chain at time t, where $X(t) = (n, \mathrm{A})$ (respectively (n, B)) denotes the state in which there are n animals on site A and the focal animal is currently on site A (respectively site B). Assume the initial value of n is in the set $\{n_{\mathrm{L}}, \ldots, n_{\mathrm{U}}\}$. Then the process $\{X(t)$: $t = 0, 1, 2, \ldots\}$ is a Markov chain with state space $\{n_{\mathrm{L}}, \ldots, n_{\mathrm{U}}\} \times \{\mathrm{A}, \mathrm{B}\}$ and stationary transition probabilities:

$$\left.\begin{aligned}
&P(X(t+1) = (n-1, \mathrm{A}) \mid X(t) = (n, \mathrm{A})) = (n-1)/2N\\
&P(X(t+1) = (n, \mathrm{A}) \mid X(t) = (n, \mathrm{A})) = 1/2\\
&P(X(t+1) = (n+1, \mathrm{A}) \mid X(t) = (n, \mathrm{A})) = (N-n)/2N\\
&P(X(t+1) = (n-1, \mathrm{B}) \mid X(t) = (n, \mathrm{A})) = 1/2N
\end{aligned}\right\} \quad n = n_{\mathrm{L}} + 1, \ldots, n_{\mathrm{U}} - 1$$

$$\left.\begin{aligned}
&P(X(t+1) = (n-1, \mathrm{B}) \mid X(t) = (n, \mathrm{B})) = n/2N\\
&P(X(t+1) = (n, \mathrm{B}) \mid X(t) = (n, \mathrm{B})) = 1/2\\
&P(X(t+1) = (n+1, \mathrm{B}) \mid X(t) = (n, \mathrm{B})) = (N-n-1)/2N\\
&P(X(t+1) = (n+1, \mathrm{A}) \mid X(t) = (n, \mathrm{B})) = 1/2N
\end{aligned}\right\} \quad n = n_{\mathrm{L}} + 1, \ldots, n_{\mathrm{U}} - 1$$

$$\left.\begin{aligned}&P(X(t+1)=(n,\mathrm{A})\mid X(t)=(n,\mathrm{A}))=1/2+n/2N\\&P(X(t+1)=(n+1,\mathrm{A})\mid X(t)=(n,\mathrm{A}))=(N-n)/2N\end{aligned}\right\}n=n_{\mathrm{L}}$$

$$\left.\begin{aligned}&P(X(t+1)=(n-1,\mathrm{A})\mid X(t)=(n,\mathrm{A}))=(n-1)/2N\\&P(X(t+1)=(n,\mathrm{A})\mid X(t)=(n,\mathrm{A})=1/2+(N-n)/2N\\&P(X(t+1)=(n-1,\mathrm{B})\mid X(t)=(n,\mathrm{A}))=1/2N\end{aligned}\right\}n=n_{\mathrm{U}}$$

$$\left.\begin{aligned}&P(X(t+1)=(n,\mathrm{B})\mid X(t)=(n,\mathrm{B}))=1/2+n/2N\\&P(X(t+1)=(n+1,\mathrm{B})\mid X(t)=(n,\mathrm{B}))=(N-n-1)/2N\\&P(X(t+1)=(n+1,\mathrm{A})\mid X(t)=(n,\mathrm{B}))=1/2N\end{aligned}\right\}n=n_{\mathrm{L}}$$

$$\left.\begin{aligned}&P(X(t+1)=(n,\mathrm{B})\mid X(t)=(n,\mathrm{B}))=1/2+(N-n)/2N\\&P(X(t+1)=(n-1,\mathrm{B})\mid X(t)=(n,\mathrm{B}))=n/2N\end{aligned}\right\}n=n_{\mathrm{U}}$$

Expected rate of intake in equilibrium

The detailed balance equations can be used to confirm that, for $n = n_{\mathrm{L}}, \ldots, n_{\mathrm{U}}$, the equilibrium probabilities for the chain are now given by $\pi(n, \mathrm{A}) = p(n)n/N$ and $\pi(n, \mathrm{B}) = p(n)(N - n)/N$, where $p(n)$ is defined in equation (A5). In equilibrium, the expected intake of the focal animal per unit time is thus exactly

$$\sum_{n}(\pi(n,\mathrm{A})r_{\mathrm{A}}/Nn+\pi(n,\mathrm{B})r_{\mathrm{B}}/N(N-n))=\sum_{n}p(n)\left(\frac{n}{N}\frac{r_{\mathrm{A}}}{n}+\frac{(N-n)}{N}\frac{r_{\mathrm{B}}}{(N-n)}\right)=(r_{\mathrm{A}}+r_{\mathrm{B}})/N$$

Expected total intake over two time periods

Assume, without loss of generality, that $r_{\mathrm{A}} > r_{\mathrm{B}}$, and assume the parameter values are such that $Nr_{\mathrm{A}}/(r_{\mathrm{A}} + r_{\mathrm{B}})$ takes an integer value, say m. Then, $r_{\mathrm{A}}/m = r_{\mathrm{B}}/(N - m)$, and m corresponds to the input matching distribution on site A. Consider the case where two focal animals start at time point $t = 0$, one on site A and one on site B, with an initial distribution of m animals on site A and $N - m$ animals on site B. The choice of m as the input matching distribution ensures that, over the first time period, the intakes of both animals will have exactly the same value, r_{A}/m, and in this sense both sites are equally attractive. However, using the transition probabilities above, the expected total intake over two time periods for the animal that starts on site A is given by

$$\frac{r_{\mathrm{A}}}{m}+\left[\frac{(N-m)}{2N}\frac{r_{\mathrm{A}}}{(m+1)}+\frac{(m-1)}{2N}\frac{r_{\mathrm{A}}}{(m-1)}+\frac{1}{2}\frac{r_{\mathrm{A}}}{m}+\frac{1}{2N}\frac{r_{\mathrm{B}}}{(N-m+1)}\right]$$

whereas that for the animal that starts on site B is given by

$$\frac{r_{\mathrm{B}}}{(N-m)}+\left[\frac{m}{2N}\frac{r_{\mathrm{B}}}{(N-m+1)}+\frac{(N-m-1)}{2N}\frac{r_{\mathrm{B}}}{(N-m-1)}+\frac{1}{2}\frac{r_{\mathrm{B}}}{(N-m)}+\frac{1}{2N}\frac{r_{\mathrm{A}}}{(m+1)}\right]$$

Using the fact that $r_{\mathrm{A}}/m = r_{\mathrm{B}}/(N - m)$, the difference between these expressions reduces to

$$\frac{1}{2N}\left[\left\{\frac{r_{\mathrm{A}}(N-m)}{(m+1)}+r_{\mathrm{A}}+\frac{r_{\mathrm{B}}}{(N-m+1)}\right\}-\left\{\frac{r_{\mathrm{B}}m}{(N-m+1)}+r_{\mathrm{B}}+\frac{r_{\mathrm{A}}}{(m+1)}\right\}\right]=$$

$$\frac{1}{2}\left[\frac{r_{\mathrm{A}}}{(m+1)}-\frac{r_{\mathrm{B}}}{(N-m+1)}\right]=\frac{r_{\mathrm{A}}-r_{\mathrm{B}}}{2(m+1)(N-m+1)}>0$$

Mean and variance of intake over a fixed time, T

Let $R(x)$ denote the immediate intake for the focal animal over one time period when it starts the period in state x, where the value of x is either (n, A) or (n, B) for some n in the set $\{n_{\mathrm{L}}, \ldots, n_{\mathrm{U}}\}$. For $t = 0, 1, 2, \ldots, X(t)$ denotes the state of the animal at the start of the tth time period and $R(X(t))$ denotes its intake over that period. Let $M_k(x)$ denote its expected total intake over the first k time periods when it starts at time point $t = 0$ in state $X(0) = x$; and let $V_k(x)$ denote the corresponding variance of its total intake over the k time periods. Thus $M_k(x) = E(\sum_{j=0}^{k-1} R(X(j)) \mid X(0) = x)$ and $V_k(x) = \mathrm{Var}\ (\sum_{j=0}^{k-1} R(X(j)) \mid X(0) = x)$. The random variables $R(X(k))$ are not independent, since the current intake $R(X(k))$ depends on the current state $X(k)$, which, in turn, determines the probable next state $X(k+1)$ and hence the next intake $R(X(k+1))$.

The Markov property implies that $M_k(x) = E(\sum_{j=r}^{k-1+r} R(X(j)) \mid X(r) = x)$ for each value of $r = 0, 1, 2, \ldots$, so that

$$\begin{aligned}
M_{k+1}(x) &= E\{\textstyle\sum_{j=0}^{k} R(X(j)) \mid X(0) = x\} \\
&= E\{E[\textstyle\sum_{j=0}^{k} R(X(j)) \mid X(1), X(0) = x] \mid X(0) = x\} \\
&= E\{E[R(x) + \textstyle\sum_{j=1}^{k} R(X(j)) \mid X(1), X(0) = x] \mid X(0) = x\} \\
&= R(x) + E\{E[\textstyle\sum_{j=1}^{k} R(X(j)) \mid X(1)] \mid X(0) = x\} \\
&= R(x) + E\{M_k(X(1)) \mid X(0) = x\}
\end{aligned}$$

Similarly for $V_k(\cdot)$ we have:

$$\begin{aligned}
V_{k+1}(x) &= \mathrm{Var}\ \{\textstyle\sum_{j=0}^{k} R(X(j)) \mid X(0) = x\} \\
&= E\{\mathrm{Var}[\textstyle\sum_{j=0}^{k} R(X(j)) \mid X(1), X(0) = x] \mid X(0) = x\} + \\
&\qquad\qquad \mathrm{Var}\ \{E[\textstyle\sum_{j=0}^{k} R(X(j)) \mid X(1), X(0) = x] \mid X(0) = x\} \\
&= E\{V_k(X(1)) \mid X(0) = x\} + \mathrm{Var}\ \{M_k(X(1)) \mid X(0) = x\}
\end{aligned}$$

We can thus derive the following recursions for successive calculation of the functions $M_k(\cdot)$ and $V_k(\cdot)$ in terms of the transition probabilities:

$$\begin{aligned}
M_{k+1} &= R(x) + \textstyle\sum_y M_k(y) P(X(1) = y \mid X(0) = x) \\
V_{k+1}(x) &= \textstyle\sum_y V_k(y) P(X(1) = y \mid X(0) = x) + \\
&\qquad \textstyle\sum_y (M_k(y))^2 P(X(1) = y \mid X(0) = x) - [\textstyle\sum_y M_k(y) P(X(1) = y \mid X(0) = x)]^2
\end{aligned}$$

with initial conditions $M_1(x) = R(x)$ and $V_1(x) = 0$.

Relative values of the total intake

Since the Markov chain is irreducible and aperiodic, the long-term average intake per unit time is given by the expected intake per time period under the equilibrium probability distribution – that is, $g = (r_{\mathrm{A}} + r_{\mathrm{B}})/N$. Moreover, this is exactly the intake rate per unit time predicted under the 'input matching distribution'. Let $H_k(x)$ denote the difference between the total expected intake for the focal animal over k time periods, starting in state x, and the total intake the animal would have obtained if it had received the long-term average intake g in each time unit. Then $H_k(x) = M_k(x) - kg$, and the values of $H_k(x)$ can be computed from those for $M_k(x)$ or directly from the recursion

$$H_{k+1}(x) + g = R(x) + \textstyle\sum_y H_k(y) P(X(1) = y \mid X(0) = x)$$

with initial condition $H_1(x) = R(x) - g$.

From standard Markov decision theory (Tijms, 1986), it follows that, for each state x, $H_k(x)$ converges to a finite limit, say $H(x)$, as $k \to \infty$. Thus $H(x)$ corresponds to the difference between the expected total long-term intake the focal animal would receive under the perceptual limit model (starting in state x) and the corresponding total intake predicted under the input matching distribution. In practice, this convergence occurs relatively quickly, so that $H(x)$ can be taken to represent the corresponding difference in expected total intake even over the medium term.