Environment Quality Predicts Parental Provisioning Decisions
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Environment quality predicts parental provisioning decisions

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Although avian parents appear to exhibit a variety of feeding strategies in nature, there currently exist no models or theories that account for this range of diversity. Here we present the results of a computer simulation designed to model inter-dependent parental decisions, where investment is meted out in small doses, and must be distributed over time to maximize return on investment at the end of the parental-care period. With this technique we show that the success of various simple, observed, parental rules of thumb varies with environmental resource level, and that increasing the complexity of parental decision rules does not necessarily result in increased fitness.

Keywords: parental investment; decision making; optimality modelling; computer simulation; western bluebird; *Sialia mexicana*

1. INTRODUCTION

Parents with multiple dependent offspring must decide how to divide resources among them. Empirical studies in birds have uncovered a variety of parental feeding patterns, including preferentially feeding the smallest chicks, largest or oldest chicks, chicks begging the most, and feeding in random order (e.g. Ryden & Bengtsson 1980; Reed 1981; Stamps *et al.* 1985; Forbes & Ankney 1987; Smith & Montgomerie 1991; Redondo & Castro 1992; Martins & Wright 1993; Malacarne *et al.* 1994; Kacelnik *et al.* 1995; Mondloch 1995; Price & Ydenberg 1995; Leonard & Horn 1996; Clark *et al.* 1997). Despite the large amount of published data on this topic, no proposal has yet been made for why such a variety of strategies should exist. Why should bird parents who all ostensibly face similar decision problems, choose these different solutions?

The nature of the decision process for individual allocation has been largely unexplored, as previous models of parental investment have failed to capture the sequential nature of the decision problem faced by parents who simultaneously raise multiple offspring. To avoid intractability, these models have typically been limited to treating parental investment either as a single event, or as a series of events with independent consequences for offspring fitness by assuming either sequential single offspring, multiple but identical offspring, or offspring that provide parents with fully informative solicitation signals (e.g. Parker & McNair 1979; Parker 1985; Harper 1986; Winkler 1987; Beauchamp *et al.* 1991; Godfray 1991, 1995). Here we present a model of investment decisions faced by parents, in a variety of environmental settings, who must simultaneously raise several offspring of differing ages and with differing resource needs.

The model is an iterative computer simulation that mimics the feeding, metabolism, digestion, and growth of asynchronously hatched western bluebird (*Sialia mexicana*)

chicks from hatching until fledging. Unlike previous models, which have been unable to capture the contingent nature of parental investment decisions over time, this model allows us to explore the complex relationship between a proximal behavioural decision-rule used to make moment-to-moment investment decisions and the ultimate fitness effects of this rule. In particular, we have looked at how various rules may fare under different environmental conditions. (The simulation was written in Java so that it could be run on multiple computer platforms. A demonstration version of the program can be viewed at http://www-abc.mpib-berlin.mpg.de/sim/Parental/).

2. THE BASIC SIMULATION WITH SINGLE CUES

To address this issue, we compared the performance of the following strategies.

Smallest: the parent first offers a bug to the smallest chick. If it is full, the bug is then offered to the next smallest, and so on.

Largest: the parent first offers a bug to the largest chick, then to the next largest, and so on. (Because size is highly correlated with age in asynchronously hatched chicks, preferential feeding of the largest chicks is essentially equivalent to feeding the oldest.)

Hungriest: the parent gives a bug to the chick with the greatest proportion of empty space in its stomach relative to its stomach size. (For our purposes, begging can be treated as an honest signal of need so that feeding the chick begging the most is equivalent to feeding the hungriest chick (Godfray 1991, 1995).)

Random: the parent offers a bug to a randomly chosen chick. If it is full, another chick is chosen at random, and so on.

Performance was measured as the summed weight of the chicks that eventually fledged. The true relationship between chick weight and survivorship is likely to exhibit diminishing returns, but we lack data that would allow us

to describe the exact shape of a weight versus survivorship curve. In the simulation, single-chick nests always weigh less than two-chick nests, which in turn weigh less than three-chick nests, etc., so we used a linear survivorship function that has a minimal effect on our results and still captures the expected monotonic increase in survivorship with fledge weight.

Parameters governing chick metabolism were derived from empirical data. Equations describing chick growth and metabolic rate in the simulation were generated by curve-fitting the values provided by Mock *et al.* (1991) for the growth and metabolic rates of western bluebird nestlings from hatching to fledging. We obtained the value for the proportion of metabolizable energy in each food item from Dykstra & Karasov (1993). From these three parameters, we were able to calculate the amount of food chicks must consume during each 24-hour period from hatching to fledging to maintain normal growth. These values were then used to extrapolate equations for weight-specific digestion rates and stomach sizes.

Environmental quality varied in the frequency with which parents found food (per cent of successful foraging trips), controlled by the probability p = probability (finding food at time t|food was found at $t-1$) and q = probability(failing to find food at time t|food was not found at $t-1$). Values for p and q were all those in the set $\{0.0, 0.1, \ldots, 0.9\}$. This method enabled us to vary both the mean availability of food resources and the average length of the sequences of foraging success and foraging failure, or 'patchiness,' of the resources. Although the variance in the number and weight of chicks fledged in different environments was greatly affected by this patchiness, the relative success of the different feeding strategies was not altered in the range that we measured. We therefore pooled results across patchiness according to the mean amount of food found, and used this mean as our metric of environmental quality.

(a) *Running the simulation*

We ran the simulation 500 times for each feeding strategy in the 100 environments specified by pairs of p and q as described above. The simulation worked as follows:

Four simulated chicks hatched at one-day intervals, were fed for 20 d, and then fledged. Each 24 h day was divided into 10 min intervals of simulated time, during which the following scenarios happened.

(1) Any egg due to hatch, hatched.

(2) The parent foraged, and found food with probability determined by parameters p and q. (The weight (in g) of the food items was chosen at random from the set $\{0.5, 1.0, 1.5\}$, but was restricted so that it was never larger than the current stomach size of the chicks.)

(3) If food was found, the decision strategy determined which chick to try to feed. In the case of the 'hungriest' strategy,

$$\text{hunger} = \frac{(\text{stomach capacity} - \text{stomach content})}{\text{stomach capacity}}.$$

(4) If the chosen chick had enough space in its stomach for the food, it was fed, otherwise the chick with the

next highest value on the criterion was chosen, and this step was repeated until a chick was fed or it was determined that all of the chicks were full.

(5) If a chick was fed, the food was added to its stomach.

(6) Each chick with food in its stomach digested 10 min worth of that food:

(i) if chick weight was less than 5.11 g, amount digested $= 0.0172$ g;

(ii) if chick weight was $\geqslant 5.11$ g, amount (in g) digested $= -0.0152 + 0.0065 \times \text{weight} - 0.0001 \times \text{weight}^2$; or the maximum amount of food in the chick's stomach, whichever was smaller;

and gained weight accordingly:
weight gain $= (0.2849 \times ((\text{grams digested}) \times (0.9792)) \times (\text{weight}/(0.0836 \times \text{weight}^{1.37}).$

(7) Every chick burned 10 min worth of calories in accordance with its metabolic rate:

energy burned $= ((0.9240 \times \text{weight}^{1.28}) \times 0.2390)/144,$

and lost weight accordingly:
weight loss $= (\text{energy burned} \times 0.2849) \times (\text{weight}/(0.0836 \times \text{weight}^{1.37}).$

(8) If a chick grew, its stomach capacity increased to accord with its new size:

stomach capacity $= 2 + \text{weight}/3.$

(9) If a chick's weight dropped below 75% of the average expected weight for its age, computed via a curve-fitting function, it died:

minimum weight $= 0.75 \times (2.3507 + (2.8003 \times \text{age}) - (0.0355 \times \text{age}^2) - (0.0020 \times \text{age}^3)).$

A flow chart of the main loop in the program is presented in figure 1. Parents foraged for 14 h each day. As with real bluebirds, during the night no food was gathered or distributed, but chicks continued to digest and grow (steps (6)–(9)).

(b) *Single cue results*

Environmental quality had a strong effect on the success of the simple feeding rules (figure 2). For all feeding rules, total fledged chick weight increases with increasing food availability. In environments in which food was found 30% of the time or less, preferentially feeding the largest chick was the most successful decision rule. 'Largest' was significantly more successful than 'Smallest', the second best rule for the 20–30% food availability range (Kruskal–Wallis, $T_{\min} = 0$, $N = 10$, $p < 0.05$). 'Largest' also outperformed all the other strategies in all of the environments with non-zero chick survivorship in the 0–19% food availability range.

For environments with 30–70% food availability, 'Smallest' outperformed all of the other strategies. 'Smallest' was significantly different from 'Random', the second most successful strategy, in the 30–40% food availability range (Kruskal–Wallis, $T_{\min} = 0$, $N = 13$, $p < 0.05$), and in the 50–60% and 60–70% ranges (50–60%: Kruskal–Wallis, $T_{\min} = 1$, $N = 22$, $p < 0.05$; 60–70%: Kruskal–Wallis, $T_{\min} = 0$, $N = 13$, $p < 0.05$). It performed better than 'Largest', the second best strategy in the 40–50% range, but not significantly so (Kruskal–Wallis, $T_{\min} = 57$, $N = 15$, $p < 0.05$).
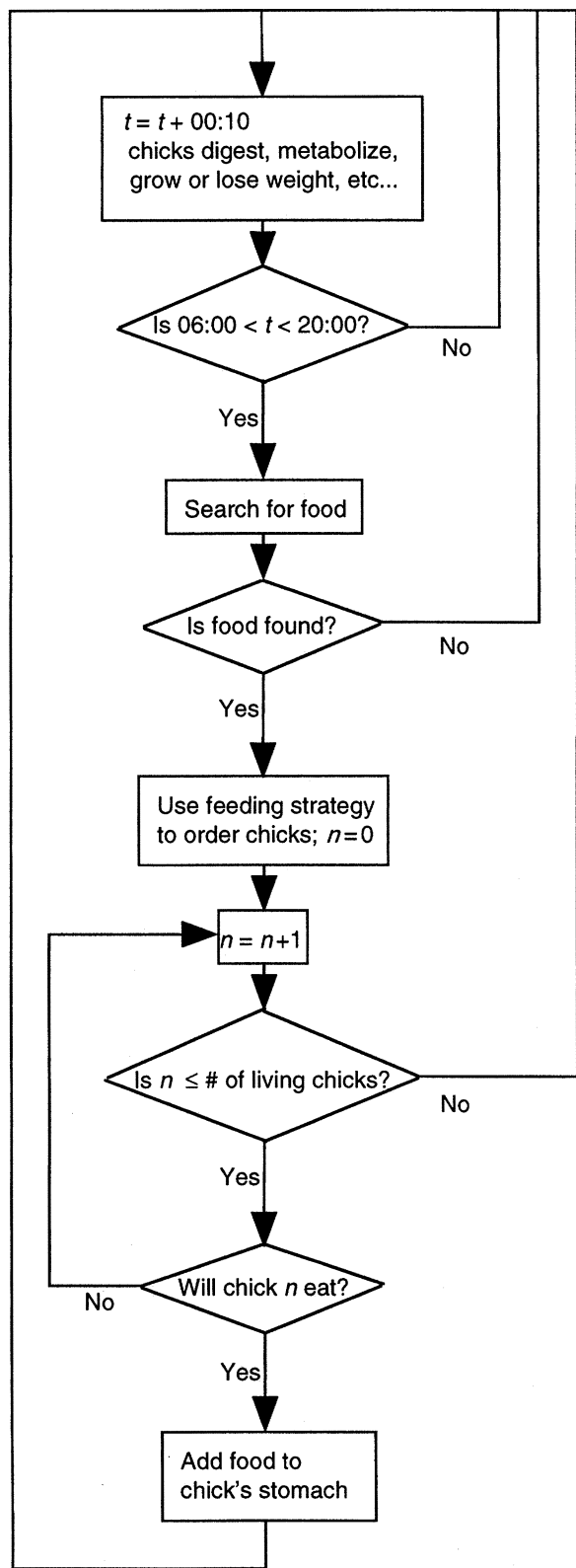
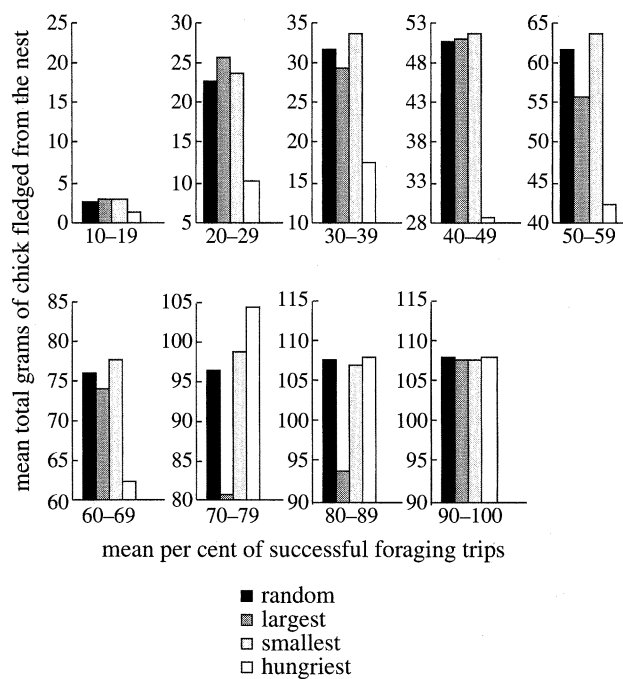Figure 1. A flow diagram of the main loop in the program.

Figure 2. The mean nest weight achieved by four simple strategies across eight ranges of environments. These environments were grouped by food availability, or the mean percentage of successful foraging attempts. The success of random feeding can be thought of as a baseline, as strategies that fail to do better than randomness are unlikely to be selected for. With random feeding, in the range 0–29% food availability, at most one chick can survive; from 30–69%, two or three can live; above this, it is possible for all four to fledge; and above 80%, all four almost always fledge. The results depicted remain qualitatively the same for clutches of three or five chicks.

In environments with 70–80% food availability, feeding on the basis of short-term need, i.e. 'Hungriest', was the most successful strategy. 'Hungriest' did significantly better than 'Smallest', the second best strategy in this range (Kruskal–Wallis, $T_{min} = 0$, $N = 9$, $p < 0.05$). 'Hungriest' was also the best strategy in the 80–90% range, and performed significantly better than 'Random', the second best strategy (Kruskal–Wallis, $T_{min} = 0$, $N = 8$,

$p < 0.05$). The magnitude of this difference was, however, very small, of the order of 0.125 g per chick. When food was even more abundant, all decision rules performed equally well. The largest per chick difference between the two best strategies was just 0.01 g.

'Largest' does particularly well in very poor environments where only one chick can be raised, because it targets a single chick for preferential investment. Because preferentially feeding the smallest chick is likely to make it full often, and can make it grow to such an extent that a sibling becomes the new smallest chick, 'Smallest' is a more egalitarian strategy (spreading food among more chicks), and it becomes successful as food resources increase. 'Hungriest' is even more egalitarian (resources are divided among *all* chicks), because the hungriest chick is continually changing, and this strategy is the most successful when all chicks can be raised. A measure of the relative egalitarianism of the different strategies across the full range of environments is provided in table 1. Although we expected 'Random' to be as egalitarian as 'Hungriest', the table shows that this is not always the case. We believe the greater weight of young chicks with random feeding is due to the greater rate at which larger chicks (which require more food per day) may starve to death when randomly skipped for too many feedings.

These results accord with the few published reports of species switching provisioning rules as a result of changing environmental conditions. Pied flycatcher females

Table 1. *Chick mean grams, the weight of each chick at the end of the simulation run, averaged across runs (the fledge weight for all chicks that survived until fledging, and 0 for all chicks that died before then); more egalitarian strategies, like 'Hungriest', have relatively equal values for each of the four chicks in the row compared with relatively inegalitarian strategies, like 'Largest', which show much larger differences*

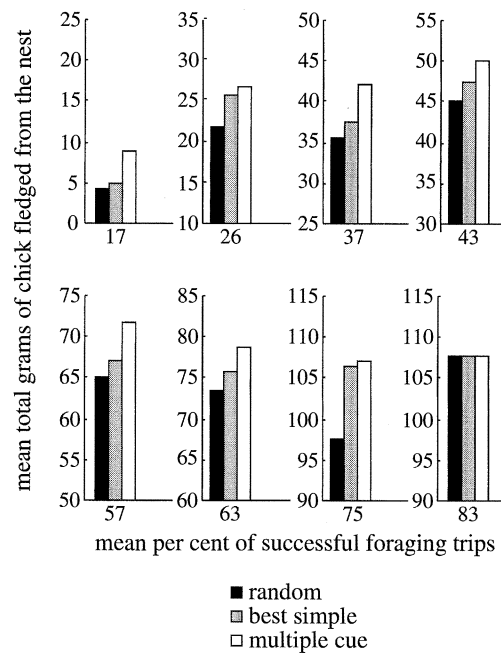| mean % successful foraging trips	feeding strategy	chick 1 mean grams	chick 2 mean grams	chick 3 mean grams	chick 4 mean grams
10–19	random	0.13	0.38	0.85	1.18
	largest	3.10	0	0	0
	smallest	0	0	0.31	2.61
	hungriest	0.20	0.17	0.20	0.63
20–29	random	1.31	2.97	5.61	9.52
	largest	22.14	0.04	0	0
	smallest	0	0.13	4.02	16.20
	hungriest	2.75	1.99	1.52	2.43
30–39	random	3.88	6.03	8.89	12.81
	largest	26.47	2.82	0.01	0
	smallest	0.10	2.38	12.18	18.86
	hungriest	5.62	5.03	3.70	3.11
40–49	random	7.67	10.89	14.20	17.71
	largest	26.95	24.09	0	0
	smallest	1.74	8.09	18.45	23.41
	hungriest	5.31	7.10	7.94	8.04
50–59	random	11.56	13.65	16.09	18.75
	largest	26.87	25.29	2.21	0
	smallest	6.45	13.93	19.09	22.78
	hungriest	5.78	9.11	11.86	14.09
60–69	random	16.44	18.13	19.96	21.39
	largest	26.96	26.87	20.16	0.01
	smallest	14.01	18.22	21.71	23.70
	hungriest	14.34	14.74	15.77	17.56
70–79	random	23.56	23.52	23.62	23.99
	largest	26.96	26.94	26.49	0.10
	smallest	23.51	23.71	24.66	25.23
	hungriest	26.04	25.85	25.79	25.84
80–89	random	26.87	26.75	26.82	26.84
	largest	26.96	26.95	26.91	12.98
	smallest	26.57	26.68	26.75	26.87
	hungriest	26.95	26.95	26.94	26.95

Figure 3. The mean nest weight achieved by the best of the multiple cue strategies across environments. These strategies preferentially fed chicks by a linear weighted sum of three chick cues: ranked age, ranked weight, and ranked hunger. Random feeding and the best of the single cue strategies are included for comparison.

hunger levels in this model. However, many field studies suggest that parents do combine cues (e.g. Forbes & Ankney 1987; McRae *et al.* 1993; Malacarne *et al.* 1994; Kacelnik *et al.* 1995; Price & Ydenberg 1995; Leonard & Horn 1996; Ostreiher 1997; Kölliker *et al.* 1998), for example, feeding according to nest position, which, as larger chicks are better able to shove their smaller siblings out of the way, and may be differentially motivated to do so by the amount of food in their stomachs, is some combination of hunger and size. We therefore also tested a set of cue-combining strategies. The cues we used were weight and hunger, also employed in the single cue simulation, and age. Although these cues are highly interdependent, and may therefore seem redundant, their exact relationship is influenced by the feeding strategy. For example, preferentially feeding the oldest may be equivalent to preferentially feeding the largest, since both of these feeding rules maintain a correlation between chick weight and age. The same cannot be said, however, for preferential feeding of youngest versus smallest chicks. The youngest chick will always be the youngest, but the preferentially fed smallest chick can grow large enough to change its size rank.

The multiple cue strategies were used to feed chicks in an order determined by a linear weighted sum of the ranks of the three cues. Ranked rather than real values of cues were used to keep the model's inputs as close as possible to the information assessable by parent birds. We assume that birds can make ordinal comparisons more readily than direct value estimates.

Cue weights were drawn from the set $\{-6, -5, \ldots, 5, 6\}$. We ran the simulation 100 times for each of the 2197 possible combinations of weighted cues. Due to the large

preferentially feed their smallest chicks under normal food conditions. When food availability is experimentally reduced, however, they preferentially feed the largest chicks (Gottlander 1987). When food is plentiful, sparrowhawk mothers allocate food resources equally among all chicks. When food becomes scarce they switch to feeding the largest (Newton 1978). This model therefore provides an explanation for these empirical findings in terms of the egalitarianism of the feeding rules, and makes predictions about variation in feeding behaviour with food availability in other species.

(c) *Multiple cues*

These strategies make decisions based only on a single cue. Parents which, for example, preferentially fed the smallest chick, could not also base their decisions on

number of strategies to be compared, we tested each in only eight environments (see figure 3), chosen to keep resource 'patchiness' relatively constant while still representing a full range of food availability.

More information led to better performance: for seven out of eight of the environments (all but the richest environment tested), there was a subset of the multiple cue strategies that outperformed the single cue rules (figure 3). These differences were statistically significant (independent sample t-test comparing the best multiple cue with the best single cue rules: $p < 0.05$ for all seven environments; 17% food availability, $t = 3.22$; 26% food availability, $t = 1.96$; 37% food availability, $t = 2.98$; 43% food availability, $t = 2.22$; 57% food availability, $t = 2.93$; 63% food availability, $t = 2.79$; 75% food availability, $t = 2.17$; variance for 83% food availability was 0, and means were identical). The best multiple cue strategy in each of these environments was one in a set of between 2 and 45% (depending on the environment) of the strategies tested that all outperformed the best of the simple cue strategies.

Most of these strategies were refinements of the best single cue rules, and are understandable from the perspective of egalitarianism introduced above. For environments with less than 30% food availability, the best multicue strategies effectively favoured the largest or oldest chick. In the range of 70–80% food availability, the parents preferentially fed the hungriest chick. In the 30–70% food availability range, strategies that achieved an intermediate level of egalitarianism by feeding the smallest and hungriest, or largest and hungriest, did best. Following Cotton *et al.* (1999) we also conclude that the assumption, seen in some of the begging literature, that parents should always attend to signals of chick need (here hunger) appears to be in error. As environmental quality changes, parental egalitarianism should also change.

(d) Short-term optimization

Without knowing the maximum possible parental success score, it is difficult to assess how well these decision rules perform in an absolute sense. While calculation of this upper limit is theoretically possible after the fact, in practice it is intractable. Determination of the optimal sequence of feeding decisions a parent bird could have made requires exact knowledge of when all bugs were found and how big they were. Given this information, all possible feeding sequences must be checked (e.g. give the first bug to chick 1 and the next to chick 3..., give the first bug to chick 2 and the next to chick 3..., and so on), to find the one that leads to the highest summed, fledged chick weight. This kind of search through the tree of possible sequences results in a combinatorial explosion of possibilities, requiring the search of a decision tree with as many as 4^{1680} nodes. Birds cannot perform such calculations, and neither can our computers, so we turned to simpler approximations.

Following in the tradition of optimality modelling, we reasoned that the behavioural choices leading to maximum parental success could be approximated by short-term optimization rules that search only a limited portion of the full decision tree. These strategies rely on reasonable guesses about the near future, and on an assumption that
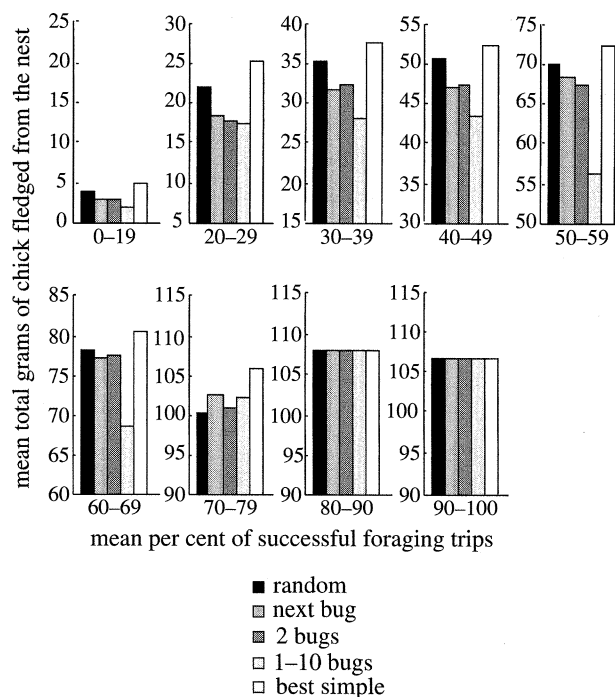

Figure 4. The mean nest weight achieved by each of the three maximizing strategies across environments. Details are as for figure 2. Random feeding and the best of the single cue strategies are included for comparison.

short-term success is an effective proxy for long-term fitness. Because they take information about the environment into account, their success should be independent of environmental conditions. In addition to each chick's real weight, age, and hunger level, the strategies we created also assume knowledge of metabolic rate, stomach capacity, and environmental parameters. All of these parameters are calculated in the course of the simulation, according to the equations presented earlier. The change here was to integrate this information into the decision strategies.

The first short-term optimization strategy selects a chick for feeding so as to maximize the summed weight attained by all chicks at the time the *next* food item is expected to be found. The second strategy maximizes summed weight at the time the *second* food item is expected. The third strategy maximizes the short-term expected value of nest weight—that is, the sum over the next ten time-steps of the probability of finding the next food item multiplied by the predicted total nest weight at that time-step. Despite the computations involved, all three maximizing strategies performed worse than the multiple cue and single cue rules, and generally worse than feeding chicks at random across all environmental conditions (figure 4).

Why are these cognitively complex optimizing strategies less successful than simple ones? One answer may be that the stochastic nature of the provisioning problem faced by many parents often leads to actions that are successful in the short-term having catastrophic impact in the longer run. In addition, their near-sightedness even as they attempt to look into the future makes the optimizing strategies rather egalitarian. As a consequence, they do worst in precisely those environments where other egalitarian strategies, such as feed the hungriest, do poorly.

3. GENERAL DISCUSSION

This model shows that environmental quality can differentially affect the success of parental provisioning strategies. The most successful strategies are all fairly simple, taking advantage of a small number of cues we expect to be readily assessable by parents. The use of different cues leads to feeding decisions that focus on a lesser or greater number of chicks, which in turn do best when food is either less or more readily available. In contrast, short-term optimizing strategies that attempt to find the single best chick to feed at each moment fare poorly across all environments.

This model has been simplified in several respects so that we can focus on the effects of particular feeding rules. We ignore biparental care, which is quite common in birds, because of the complications caused by two parents adopting different rules. We also assume that parents have full control over which chick they feed, an assumption that is at least occasionally subject to error (e.g. Kacelnik *et al.* 1995), although the degree to which nestling competition for feeding positions is truly driven by chick, as opposed to parental, preferences is not yet fully understood. These are both obvious directions in which to extend the simulation.

Given the difficulty of assessing the precise states of individual chicks, parents must use imprecise cues, such as relative rankings. Our results show that this rough information can be coupled with simple rules and still yield adaptive feeding behaviour. Environmental quality determines which simple rule is best employed. As a consequence, in those species where parental provisioning strategies are plastic, we can predict further that it should be possible to change the rules parents use by experimentally manipulating the level of food they find. By gradually changing from a restricted diet to unlimited food access, parents may be induced to switch from despotically feeding their largest offspring to a moderately egalitarian strategy such as feeding the smallest or the largest—hungriest, to the more egalitarian strategy of feeding the hungriest, and finally to feeding all offspring equally. That parents are capable of switching strategies in a manner at least consistent with our results has already been demonstrated in two studies (Newton 1978; Gottlander 1987), but further evidence must still be gathered.

Avian investment rules can potentially span a wide range of presumed cognitive abilities on the part of parents. In the simplest case, parents may use the environment to make their decisions for them by, for example, feeding at fixed nest positions and allowing the chicks to order themselves within it (e.g. Kölliker *et al.* 1998). Alternatively, parents could combine observed chick cues by using a simple fixed rule. With more sophistication, parents could choose between different simple rules, depending on the current state of the environment they face, first assessing environmental quality and then using the appropriate chick cues to make feeding decisions. It is clear that parents should be capable of making such environmentally contingent decisions. Choosing between feeding strategies requires only a means of evaluating environmental richness, a capacity that has been assumed by behavioural ecologists working on a variety of problems, including optimal foraging, which is aimed at explaining how such assessments can be made (e.g. Stephens & Krebs 1986). Finally, parents could also use a complex decision-making strategy that applies to any environment.

In focusing on the decision-making abilities of parent birds, we have left out the first case, and we have shown that the complex strategies in the last case are unlikely to work well. We are left with the possibility that birds use either fixed rules that are environment independent, or rules that are facultatively chosen by the birds themselves, depending on the current environmental circumstances. Which of these alternatives holds for a given species will depend at least in part on the past variability of environmental conditions faced during evolution. In either case, a degree of environmentally contingent simplicity appears to rule the roost.

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