

# Parental investment without kin recognition: simple conditional rules for parent–offspring behavior

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Received: 15 September 2010 / Revised: 2 November 2010 / Accepted: 4 November 2010 / Published online: 22 December 2010  
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**Abstract** Species differ widely with regard to parental investment strategies and mechanisms underlying those strategies. The passing of benefits to likely genetic offspring can be mediated through a number of different computational and behavioral systems. We report results from an agent-based model in which offspring maintain proximity with parents and parents transmit benefits to offspring without the capacity of either parent or offspring to “recognize” one another. Instead, parents follow a simple rule to emit benefits after reproducing and offspring follow a simple rule of moving in the direction of positive benefit gradients. This model differs from previous models of spatial kin-based altruism in that individuals are modeled as having different behavioral rules at different life stages and benefits are transmitted unidirectionally from parents to offspring. High rates of correctly directed parental investment occur when mobility and sociality are low and parental investment occurs over a short period of time. We suggest that strategies based on recognition and bonding/attachment might serve to increase rates of correctly directed parental investment under parameters that are shown here to otherwise lead to high rates of misdirected and wasted parental investment.

**Keywords** Conditional movement · Parental investment · Kin recognition · Parental care · Agent-based model

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Communicated by M. Hauber

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## Introduction

Parental investment exists across a wide range of taxonomic groups (Kleiman and Malcom 1981; Clutton-Brock 1991; Gubernick and Klopfer 1981). In these taxa, parental investment takes a variety of forms, and the nature and pattern of these forms have been fairly well characterized (Gubernick and Klopfer 1981; Clutton-Brock 1991; Ross 2003; Kolliker 2007; Quinlan 2007; Steinegger and Taborsky 2007; Maurer 2008; Wolovich et al. 2008; Fernandez-Duque et al. 2009; Mattle and Wilson 2009). For some taxa, there is also evidence that the behavioral tendencies leading to the transmission of benefits to offspring have a genetic basis and can, therefore, be favored by natural selection (Kappeler and Schaik 2005; Chapais and Berman 2004; Kokko and Jennison 2008; Charpentier et al. 2008). This is in support of some of the initial formulations of parental investment theory proposing that natural selection will favor the passing of benefits to genetic offspring when the costs of doing so are relatively low, the benefits relatively high, and the likelihood of relatedness high enough (Hamilton 1964a, b; Trivers 1972; Maynard Smith 1977).

Even when ultimate evolutionary explanations for the existence of parental investment may be resolved for a given taxon, it is usually the case that we lack a similar understanding of the mechanisms and processes regulating parental investment. Any instance of parental investment must be somehow realized by proximate cognitive and behavioral mechanisms that enable parents to transmit benefits to offspring. There has been a long history of work on kin recognition (e.g., Holmes and Sherman 1983; Sherman and Holmes 1985; Waldman 1988; Waldman et al. 1988; Neff and Gross 2001; Alvergne et al. 2009; Dubas et al. 2009), but the proximate mechanisms underlying the discriminatory provisioning of parental investment towards

kin are not always well understood. For example, kin recognition mechanisms such as phenotypic matching, the presence of recognition alleles, and learning of kin characteristics could enable selective transmission of benefits to offspring (Hepper 1991; Halpin 1991; Reeve 1989; Tang-Martinez 2001; Hauber and Sherman 2001). Each of these requires relatively complex cognitive and behavioral capacities. Still, it is possible that under certain circumstances, parental investment can be correctly directed to offspring in the absence of recognition abilities or other complex cognitive processes (Peterson 2000; Anderson and Hauber 2007; Grim 2007; Green et al. 2008; Stynoski 2009; Riehl 2010). In other words, there may be simple mechanisms leading to parental investment that do not require kin recognition. Under the proper ecological conditions, simple rules based on spatial location or reproductive status may still be effective (Holmes and Sherman 1983; Sherman and Holmes 1985; Waldman et al. 1988; Green et al. 2008).

### Proximity and parental investment

Spatial proximity between parents and offspring has the potential to function as a relatively simple mechanism for adaptive parental investment. The transmission of benefits from parents to offspring typically requires spatial proximity between them. Incubation, lactation, regurgitation, food sharing, carrying, and protection are all forms of parental investment requiring that offspring and parents maintain proximity (Kleiman and Malcom 1981; Clutton-Brock 1991).

The acknowledgment of the importance of spatial proximity in parental behavior is not new in the literature. The maintenance of spatial proximity between offspring and caretaker is the central concept in attachment theory and is a well-described phenomenon. In attachment theory, one of the main benefits of maintaining spatial proximity is thought to be increased protection from predators (Bowlby 1969; Mason and Mendoza 1998). It has also been noted that spatial proximity can enable the selective transmission of benefits to offspring, such as food, warmth, and various kinds of sensory stimulation (Gubernick and Klopfer 1981).

However, offspring might not always be near, and the indiscriminate provision of benefits to those who happen to be nearby can lead to misdirected or wasted parental investment. Among group living species (e.g., colonial or herd living species) and those with high mobility, there may be more opportunities for “mistakes” in the transmission process so that benefits are transmitted to non-offspring. It has been suggested that the long-term social recognition associated with “attachment” might function as a mechanism to reduce those potential errors (Gubernick and Klopfer 1981). Likewise, in species with lower mobility

or those that are less social, mechanisms of social attachment might be unnecessary for the effective and accurate transmission of benefits to offspring.

Here, we ask whether the ability to maintain spatial proximity can enable correctly directed parental investment, even in the absence of complex decision rules or specialized sensory/perceptual systems. It is true that proximity can be maintained through a variety of complex physiological, behavioral, and cognitive mechanisms including recognition systems (Hepper 1991; Halpin 1991; Tang-Martinez 2001; Hauber and Sherman 2001), bonding (Uvnäs-Moberg et al. 1994), attachment (Bowlby 1969), clinging/carrying abilities, and other capacities, but these complex systems may not be necessary for accurate parental investment. In organisms such as plants and bacteria, non-cognitive systems underlie kin discrimination. For example, plants are known to exude soluble chemicals through their roots that act as kin markers; the root exudates of kin inducing less root formation and, therefore, less competition with kin than the exudates of strangers (Biedrzycki et al. 2010). There is also evidence in more cognitively complex organisms for the use of simple rules that promote correctly directed investment (Stynoski 2009; Green et al. 2008).

We model a very simple decision rule that maintains parent–offspring proximity: offspring follow the gradient of benefits emitted by their parents. Offspring are able to perceive the level of benefits on their current location and on the location immediately in front of them, moving forward only if the level of benefits is higher in the location ahead (else they turn around and repeat the process during the next time step). Our model allows us to explore whether this simple rule that does not involve kin recognition or memory can lead to correctly directed parental investment. Further, we explore the limits of this rule’s viability by exploring its performance under a variety of ecological and social conditions. By identifying conditions under which this simple rule does not lead to correctly directed parental investment, we gain some understanding of the ecological and social conditions that are likely to favor the evolution of more complex rules for parental investment.

### Models of parental investment and altruism

A variety of primarily qualitative theoretical models of the evolution of parental investment have been proposed which have focused on the viability of parental investment and strategic concerns associated with bi-parental care (Trivers 1972; Maynard Smith 1977; Dawkins and Carlisle 1976; Lancaster and Lancaster 1983; Hamilton 1984; Kurland and Gaulin 1984; Kokko and Jennison 2008; Kokko et al. 2006). Qualitative and mathematical models such as these have provided traction for understanding the cost–benefit tradeoffs inherent in parental investment decisions but are less

effective for exploring the viability of various mechanisms that might underlie parental investment. On the other hand, simulations provide a way of exploring and testing the functional and evolutionary viability of various mechanisms that can underlie behaviors such as parental investment.

Despite a relative dearth of spatial simulations of the viability of parental investment *per se* (but see Lion and van Baalen 2007), a number of models of the evolution of cooperation/altruism have addressed topics that are relevant to the evolution of parental care. Simulations have, for example, investigated the viability of cooperative behavior in populations with various kinds of mobility (Aktipis 2004; Brauchli et al. 1999; Enquist and Leimar 1993; Ferriere and Michod 1996; Marshall and Rowe 2003; Mitteldorf and Wilson 2000) and in situations where individuals can use individual recognition (Vos and Zeggelink 1994; Cox et al. 1999; Aktipis 2006) or even the recognition of arbitrary tags (Axelrod et al. 2004). If parental investment is considered a type of altruism, models such as these could be used to draw conclusions about the viability of parental investment. For instance, cooperative/altruistic strategies tend to be successful in stable population structures and when individuals can use recognition memory. If these same principles are valid in relationship to the passing of benefits from parents to offspring, mobility and recognition would play important roles in parental investment strategies.

Modeling parental investment as a form of altruism or cooperation requires certain considerations and assumptions. Offspring are typically the recipients of benefits and might never “reciprocate” by directly passing benefits back to a parent (although offspring contribute to the inclusive fitness of parents). This unidirectional passing of benefits is not captured by traditional models of reciprocal altruism, and other potential differences between parents and offspring are abstracted away in most models. The maintenance of spatial proximity is also an important component of parental investment strategies that is only peripherally captured by spatial (e.g., Brauchli et al. 1999; Nowak and May 1992; Ifti et al. 2004) and network models (e.g., Ohtsuki et al. 2006; Lehmann et al. 2007; Taylor et al. 2007) of the evolution of cooperation. Models have also explored the ways in which spatial structure and proximity emerge from the interactions of organisms with each other and with a shared environment (Ramos-Fernández et al. 2006).

We present here an agent-based model (Wilensky 1999; Grimm et al. 2006; Grimm and Railsback 2005) that investigates the effectiveness of a parental investment system that does not make use of social recognition but relies instead on relatively simple rules. Using an agent-based model based on simple rules that promote proximity maintenance between parents and offspring, we explore whether those rules lead to correctly directed parental investment under certain social and ecological conditions. We use a spatial agent-based model in

order to allow for spatial interactions between parents and offspring. This model allows us to explore the viability of simple proximity maintenance mechanisms that can promote correctly directed parental investment. By exploring parameters under which these simple rules for parent/offspring behavior can generate effective parental investment and those under which they falter, it becomes possible to outline the ecological and social factors that might favor more complex systems for directing parental investment.

Specifically, in this model, offspring use conditional movement rules to maintain proximity to entities (i.e. parents) emitting benefits. It has been suggested that conditional movement may be considered one of the fundamental building blocks of behavior, operating on the most basic types of information that are available in an organism’s environment (Aktipis 2008). Here, we apply those principles to the examination of parent–offspring behavior, and we provide an agent-based model that shows how certain aspects of parent–offspring behavior can be instantiated with conditional movement and benefit transmission rules.

In this model, we explore the effects of mobility, sociality, density, and length of parental investment on correctly directed, misdirected, and wasted parental investment. We predict that increased mobility (likelihood of moving per time period), sociality (probability of entering an occupied patch), and density (number of individuals per unit space) will decrease the amount of correctly directed parental investment by decreasing the likelihood that parents and offspring will remain in proximity. Similarly, long periods of parental investment should decrease the likelihood that parents and offspring will remain in proximity, decreasing the amount of correctly directed parental investment.

## Model description

The description follows the standardized Overview, Design concepts, Details (ODD) protocol for describing individual and agent-based models (Grimm et al. 2006; Grimm and Railsback 2005). The ODD protocol was designed with extensive input from 20 agent-based modelers from a variety of disciplines in order to provide a clear and complete description of agent-based models. Because agent-based models have many components and lack the operational simplicity of mathematical models, they can be difficult to describe comprehensibly and completely in a standard methods section. The introduction of the ODD protocol provides a standard presentation that is logical, well organized, and complete. This protocol is in wide use in diverse fields, from ecology to land-use modeling.

Our model was built using NetLogo 4.0.2 (Wilensky 1999), an agent-based modeling platform designed for

simulating natural and social phenomena. This platform has a built-in user interface with a spatial grid. Importantly, Netlogo allows the modeler to create an intuitive user interface, allowing other researchers to easily use the model regardless of modeling expertise. The full model and documentation can be downloaded at the Open Agent-Based Modeling website (<http://www.openabm.org/model-archive/aktipispi>), and free Netlogo software is available at <http://ccl.northwestern.edu/netlogo/>.

### Purpose

This model was developed to explore the parameters under which simple rules promoting parent–offspring proximity can lead to the transmission of benefits from parents to genetic offspring, that is, correctly directed parental investment (PI). In the model, parents simply emit benefits and offspring follow positive benefit gradients, leading to proximity maintenance under some conditions. The model explores the effects of mobility, sociality, density, and length of PI. We can then speculate that strategies based on recognition and bonding/attachment might serve to increase rates of correctly directed PI under parameters that are shown here to otherwise lead to high rates of misdirected and wasted PI.

### State variables and scales

Time and space are both represented discretely. Space is represented as discrete locations in a one-dimensional line made of 201 lattice locations or “patches.” Movement of parent agents along this line is determined by their movement propensity, offspring movement is determined by their benefit approach rule. During each time step, agents and patches execute the commands described in the schedule.

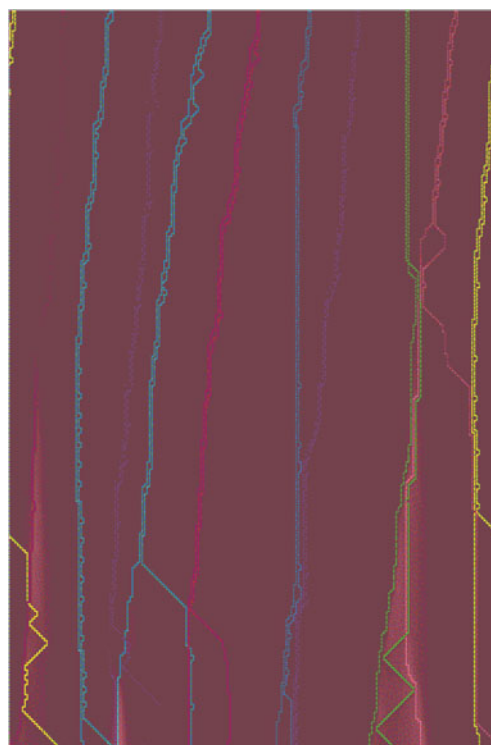
As time advances, the system moves down, as in a standard cellular automaton model (Fig. 1). This enables visualization of the behavior of the system over time.

There are four kinds of entities: global variables, which are associated with the overall state of the system (e.g., the number of agents), patches (unique lattice locations), and two types of agents (parents and offspring). Table 1 provides a full description of the state variables associated with each of the entities.

### Process overview and scheduling

The model proceeds in discrete time steps, and entities execute procedures in the following order (a more detailed schedule is provided in Appendix 1):

1. Resources diffuse between neighboring patches.
2. Parents produce energy, adding to the resources on the current patch.



**Fig. 1** Screenshot of a simulation using the default parameters. The simulation begins at the top and the world (a horizontal line with 201 locations) and agents move down as time progresses, leaving a visual record of their movement over time. Offspring are initially placed in the patch immediately to the right of their parents (at the top of the figure), and after that parents and offspring move according to the schedule and rules described below. Parents emit energy every time period in the patch immediately to their right, and offspring consume this energy. Remaining energy diffuses over time, and patches with energy (resources) on them are indicated by a lighter pink hue

3. Agents move.
  - a. Parents move according to mobility and change heading according to turn propensity.
  - b. Offspring follow benefit approach rule.
4. Offspring consume resources from the current patch.

### Design concepts

*Emergence* Parent–offspring proximity emerges from the simple individual-level rules being used by the agents. When this proximity is achieved, it results in correctly directed PI, also an emergent phenomenon.

*Adaptation* No evolutionary adaptation occurs.

*Fitness* Although parental and offspring fitness are not explicitly modeled, the level of correct PI may positively correlate with fitness in certain ecological and social circumstances in which the model may be applied.

**Table 1** Overview of state variables associated with each type of entity

Entity	State variable	Description
Global	<b>Number of pairs</b>	Number of parent–offspring pairs included in simulation. Higher values indicate higher density.
	<b>Sociality</b>	Likelihood that an agent will enter an already occupied patch
	Diffusion	Rate at which benefits diffuse to neighboring patches
	<i>Correct PI</i>	Number of time periods in which a parent places benefits on a patch occupied by offspring
	<i>Misdirected PI</i>	Number of time periods in which a parent places benefits on a patch occupied by non-offspring
Patches	<i>Wasted PI</i>	Number of time periods in which a parent places benefits on an unoccupied patch
	Location	Coordinates of the patch
Agent-parent	Resource	Amount of energy on current patch
	<b>Mobility</b>	Percentage likelihood of moving 1 unit each time step
Agent-offspring	Turn propensity	Percentage likelihood agent changes direction
	Benefit provision	Amount of energy parent places on patch immediately to the right per time step
	Heading	Direction of agent movement
	Location	Coordinates of agent
	Consumption amount	Amount of energy offspring consume from current patch per time step
Agent-offspring	Heading	Direction of agent movement
	Location	Coordinates of agent

Bold indicates the independent variable and italicized entries indicate dependent variables

*Prediction* Agents lack the ability to predict outcomes of future interactions or integrate information across time steps.

*Sensing* Offspring have the ability to sense the resource level on the current patch and the patch immediately ahead.

*Interaction* Parents and offspring interact indirectly through the shared environment (i.e., the passing of benefits from parents to offspring through patches).

*Stochasticity* Parental mobility, turn propensity, and sociality are modeled probabilistically.

*Collectives* Parent–offspring pairs can be considered collectives, but they do not have aggregate variables associated with them.

*Observation* In the first three experiments, 100 independent runs (of length 2,000 time steps) took place for each parameter value being explored (Table 2). The amount of correctly directed, misdirected, and wasted PI is reported at

**Table 2** Initial and default values for all variables

Entity	State variable	Initial/default value	Units
Global	<b>Number of pairs</b>	10	Count
	<b>Sociality</b>	1%	% Likelihood
	Diffusion	.5	Rate
	<i>Correct PI</i>	0	Count
	<i>Misdirected PI</i>	0	Count
Patches	<i>Wasted PI</i>	0	Count
	Location	(–25–25, –25–25)	Coordinates
Agent-parent	Resource	0	Energy
	<b>Mobility</b>	10%	% Likelihood
	Turn propensity	5%	% Likelihood
	Benefit provision	.05	Energy
	Heading	90°	Degrees
Agent-offspring	Location	Random along line	Coordinates
	Consumption amount	.05	Energy
	Heading	90°	Degrees
	Location	To the right of parent	Coordinates

Bold indicates the independent variable and italicized entries indicate dependent variables

the end of each run and averaged across all 100 runs. The fourth experiment reports correctly directed, misdirected, and wasted PI every time step for 2,000 time steps, averaged across 30 runs.

### Initialization

All runs were initialized according to default parameters as shown in Table 2.

### Input

The model has been designed as a general model of PI that may apply across a variety of taxa. Parents emitted benefits locally and offspring consumed benefits locally, so spatial proximity of parents–offspring pairs resulted in PI. This is consistent with the observations that spatial proximity can enable the selective transmission of benefits to offspring including food, warmth, and various kinds of sensory stimulation (Gubernick and Klopfer 1981). It could also be generalized to include the benefits associated with protection from predators (Bowlby 1969; Mason and Mendoza 1998). These observations about PI in various taxa provided a basis for the assumptions of this model. Our operationalization of parental investment fits the definition of Trivers (1972) of parental investment as a rivalrous investment in offspring. Parents transmit benefits for a limited number of time periods and, therefore, incur an opportunity cost when transmitting benefits to offspring. This makes our model applicable to situations that meet these criteria, rather than a broader and more poorly defined class of parent–offspring interactions (e.g., parental behavior or parental care).

## Experiments and results

Each experiment reported below is a set of runs investigating a particular set of parameter values. More details regarding the

data collection can be found in the “observation” section in design concepts in the model description. When parents placed benefits on a patch that had their genetic offspring, this was considered correct PI. When parents placed benefits on a patch occupied by a non-offspring, this was considered misdirected PI. If parents placed benefits on a patch that was not occupied this was considered wasted PI.

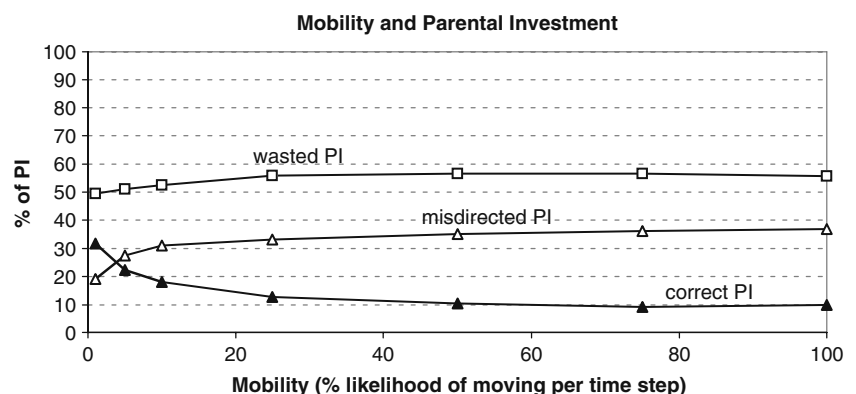
### Experiment 1: effects of mobility

There was a straightforward relationship between parental mobility and PI. As mobility increased, correctly directed PI decreased and misdirected PI increased (Fig. 2). Only at very low levels of mobility was correctly directed PI greater than misdirected PI, suggesting that increases in parental mobility have dramatic effects on the effectiveness of PI. Wasted PI was high for all levels of mobility and wasted PI did increase slightly as mobility increased.

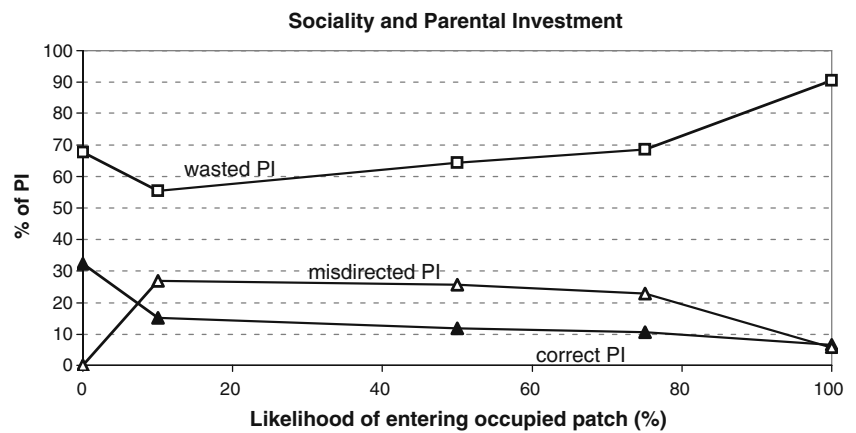
### Experiment 2: effects of sociality

Sociality was defined as the likelihood that agents would enter an already occupied patch. In other words, sociality can be considered the tolerance of an agent to high density. Sociality was clearly associated with changes in the patterns of PI (Fig. 3). When agents did not enter occupied patches (sociality=0), the rate of misdirected PI was 0 and the rate of correct PI was at its highest level (32.2%). Correctly directed PI occurred only with very low levels of sociality; when sociality increased, the rate of misdirected PI increased dramatically. Misdirected PI increased as sociality increased and then decreased as sociality reached 100%. When sociality was 100%, wasted PI was very high (90.6%), a result that may be due to a modeling artifact. Since there are fewer occupied patches when sociality is high, and parents place benefits on the patch to their right, is it more likely to place benefits in an unoccupied patch when sociality is high.

**Fig. 2** Relationship between mobility and percentage of correct, incorrect, and wasted parental investment



**Fig. 3** Relationship between sociality (likelihood of entering an occupied patch) and percentage of correct, incorrect, and wasted parental investment



#### Experiment 3: effects of density

The density of parent–offspring pairs was related to changes in PI (Fig. 4). Low densities resulted in low levels of misdirected PI. The highest level of misdirected PI occurred at intermediate densities. Correctly directed PI occurred at moderate levels when densities were high and low, but not when densities were intermediate. Higher densities led to fewer instances of wasted PI, because higher densities made it less likely that the benefits would be placed on an unoccupied patch.

#### Experiment 4: effects of length of investment period

Figure 5 shows the cumulative rates of each type of PI (Fig. 5a–c) averaged over 30 runs. The slope of each line represents the rate of change in instances of correct, misdirected, and wasted PI as time increases. When mobility was low (1%), cumulative correct PI increased for approximately 800 time steps (5a). At intermediate mobility (10% chance of moving each time step) cumulative correct PI increased for only about 400 time steps (5b). Finally, at high levels of mobility (50% chance of moving each time step), cumulative correct PI began to plateau after

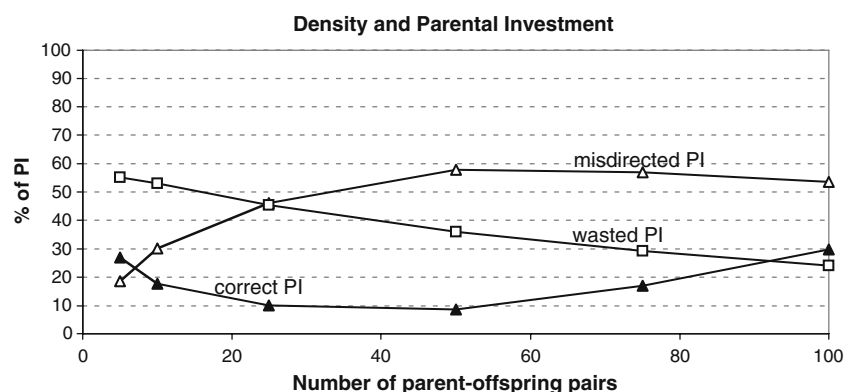
only about 200 time steps (5c), and misdirected and wasted PI increased quickly.

These results indicate that PI over shorter time scales was more accurate than reflected by the data presented in experiments 1–3. By examining the change in cumulative PI over time, we determined that correctly directed PI had an initial period of linear increase and then reached an asymptote as offspring became separated from parents. Wasted PI and misdirected PI were initially zero but began to increase as correctly directed PI reached the asymptote. The pattern described for correctly directed PI was observed for three different levels of mobility, with lower levels of mobility corresponding to longer periods of correct PI.

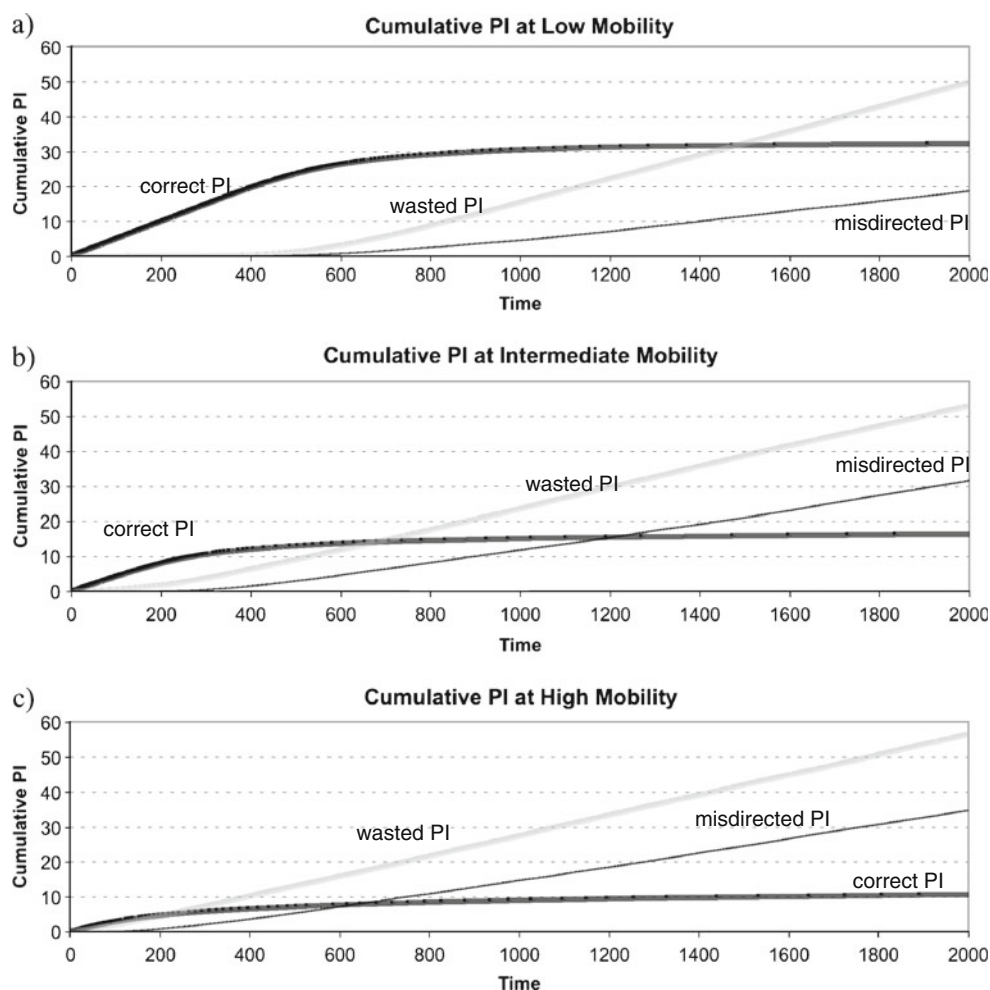
#### Discussion

Our results demonstrate that parents can preferentially transmit benefits to offspring without necessarily having mechanisms for kin recognition. It is known that kin discrimination, or differential treatment of conspecifics based on correlates of genetic relatedness, can occur in the absence of processes for directly assessing genetic

**Fig. 4** Relationship between density (number of parent–offspring pairs) and percentage of correct, incorrect, and wasted parental investment



**Fig. 5** Cumulative parental investment at **a** low mobility (1%), **b** intermediate mobility (10%), and **c** high mobility (50%)



relatedness (Waldman 1988; Barnard et al. 1991; Holmes 2004; Alvergne et al. 2009; Neff and Sherman 2003). Spatial discrimination (i.e., treating individuals within a certain range as kin) has been suggested as a viable mechanism for parental investment (Holmes and Sherman 1983; Sherman and Holmes 1985). For example, Komdeur and Hatchwell (1999) suggest that spatially based mechanisms such as “feed anything in my nest or territory” may be the simplest way to confer discriminative provisioning to offspring. However, it has been argued that this kind of spatially based provisioning should not be considered a recognition mechanism, because it does not require cognitive or behavioral systems that can identify kin (Halpin 1991; Tang-Martinez 2001). Our model can be considered an instantiation of very simple spatially based provisioning. In the present model, parents simply emit benefits locally and offspring maintain proximity to parents by following the benefit gradient. These simple rules led to correctly directed parental investment in certain ecological and social conditions.

In the model we presented, the parameters that we explored affected parental investment in ways that are largely consistent with the literature. Mobility, sociality,

density, and the length of parental investment were all influential in the outcomes of the model. The model generated higher levels of correct parental investment with low mobility, low sociality, high and low density, and short periods of parental investment. Overall, the model generated the highest rates of correctly directed parental investment under conditions that resulted in a relatively close proximity between parents and offspring.

In our model, parental investment was considered wasted if parents placed benefits on an unoccupied patch. It is worth noting that under many ecological and social conditions, there would be strong selection pressures against this type of indiscriminate benefit provisioning. Further, it is likely to be easy for parents to evolve the ability to recognize whether a potential location is occupied or unoccupied. However, this model was designed to explore the simplest possible decision rules that might underlie parental investment. Modifications to make the rules more complex are likely to be a fruitful direction for future work and could explore the effects of species recognition, kin-based recognition, or individual recognition in benefit provisioning by parents.



## Mobility and parental investment

In our model, low mobility resulted in higher rates of correctly directed parental investment. This is consistent with evidence from field and laboratory studies of a wide range of taxa (Nalepa 1997; Peterson 2000). Among salamanders, there are significant differences in the patterns of parental care and mobility between terrestrial and semi-aquatic species. The more mobile semi-aquatic salamanders distinguish between their eggs and those of other females, while terrestrial and less mobile red-backed salamanders (*Plethodon cinereus*) have much longer periods of parental care that do not seem to require egg recognition (Peterson 2000). In cockroaches, the phylogenetic appearance of parental care (in species such as *Blattella*) is positively associated with ovoviviparity because the retention of the eggs until hatching allows for the proximity of the adults and neonates both in time and space (Nalepa 1997). Further, among the Aché of Paraguay (a traditional hunter-gatherer society in which parental mobility is likely to influence offspring survival), young children increased proximity to the mother and spent more time in tactile contact with her during mobile foraging trips (Kaplan 1996). At a more proximate level, decreased motor activity and parental behavior are both promoted through higher levels of oxytocin (Uvnäs-Moberg et al. 1994), suggesting that lower mobility and parental investment may be mediated by the same physiological system.

## Sociality

Low levels of sociality generated higher rates of correctly directed parental investment in our model. When sociality was 0 (i.e. agents could not pass over one another), there were no instances of misdirected parental investment, although rates of wasted investment could be high. It is possible to imagine that low mobility (see earlier Discussion) will be associated with low sociality in a number of taxa. If the probability of encountering other conspecifics is relatively low, this should result in an increased probability of being in close contact with offspring when parents and offspring have low mobility.

On the other hand, high levels of sociality generated misdirected investment which may seem to be an evolutionary disadvantage. However, the presence of misdirected investment with high sociality need not imply evolutionary disadvantages if individuals live in closely related groups. In species that breed in highly related groups (e.g., cooperative breeders and eusocial insects), “misdirected” investment might still promote inclusive fitness because beneficiaries are highly related even if they are not the individual’s offspring. In evolutionary terms, the costs and benefits of “correct” and “misdirected” benefit transmission

will be based on the relatedness of the recipient of the “misdirected” investment. Therefore, whether or not particular levels of “correct” and “misdirected” investment would be adaptive (i.e., be selected) will be dependent on the kin structure of the environment. If parents emit benefits that are not uniquely directed towards their own offspring, this could still be strongly selected if other recipients are closely related (as is the case in eusocial insects and some cooperative breeders).

There are numerous ecological scenarios that illustrate how different degrees of sociality may be related to the extent of parental investment. Paternal care is quite common among fish. Bluegill sunfish (*Lepomis macrochirus*) males provide regular care both to their eggs and fry and have been shown to recognize kin using direct chemical cues and to modify their care accordingly (Neff and Sherman 2003). Because this species has both parental males and cuckold males, this should result in males modifying their patterns of care based on sociality (i.e. number of cuckolders present around a parental male). Although we do not know yet if this is the case among bluegill sunfish, there is clear evidence of discriminative investment in birds. Both dunnocks (*Prunella modularis*) and barn swallows (*Hirunda rustica*) adjust the investment made in chicks in relation to paternity certainty, which is closely linked to sociality. Among these species, higher levels of sociality (colonial or polyandrous vs. monogamous) resulted in lower levels of parental investment (Neff and Sherman 2002 on recognition mechanisms).

## Density

Correctly directed investment occurred at both very high and very low densities of agents. Correctly directed parental investment resulted at low densities because at these low densities, offspring were less likely to encounter the benefit gradients generated by other parents and, therefore, more able to maintain proximity to the parent. When there was low density (five parent–offspring pairs), there were fewer nearby agents whose proximity might disrupt the parent–offspring pairs, leading to higher rates of correct parental investment and low rates of misdirected parental investment.

High densities, on the other hand, increased the level of correct parental investment for other reasons. At high density (100 parent–offspring pairs), parents were unlikely to place benefits on unoccupied patches, leading to higher rates of correct parental investment and low rates of wasted parental investment. Also, under very high densities, parent–offspring pairs were tightly packed and “held together” by neighbors on either side. Because the likelihood that agents would enter an occupied patch (sociality parameter) was very low, the result was that

tightly packed parent–offspring pairs were unlikely to get separated. This also explains why misdirected parental investment increases initially, but decreases at higher densities.

Unsurprisingly, high densities led to lower levels of wasted parental investment because offspring were less likely to wander off. As mentioned in the above section on sociality, in certain types of organisms (eusocial species), low levels of wasted parental investment may be more important than correct parental investment because of high relatedness among individuals that are part of a group. We speculate that one of the benefits of grouping together tightly may be dramatic decreases in wasted parental investment. Among social insects, non-reproductive workers transmit benefits to non-offspring (but highly related colony members). The case of eusocial insects appears to be one in which this behavior of transmitting benefits to non-offspring was selected, due to factors including kin structure, resource structure, and reproductive suppression of workers by fertile queens (Hölldobler and Wilson 2009).

#### Length of parental investment

We demonstrated that shorter lengths of parental investment result in higher levels of correct investment and lower levels of misdirected and wasted parental investment. These results suggest that, *ceteris paribus*, longer periods of parental investment might be more viable in species with relatively low mobility. Of course, the addition of more complex strategies for parental investment might allow long periods of parental investment to occur with fewer errors. Furthermore, the kin structure of the social world can influence the viability of long periods of parental investment (Galef 1981; Kleiman and Malcom 1981). As suggested above, when all potential recipients are highly related, misdirected investment might not be costly in terms of inclusive fitness.

The optimal length of parental investment is a question of interest in a number of topic areas within evolutionary biology including work on life history theory (MacArthur and Wilson 1967; Daly and Wilson 1983; Kaplan and Gangestad 2005), parental investment theory (Trivers 1972; Maynard Smith 1977; Wade and Shuster 2002), and parent–offspring conflict (Pugesek 1990; Queller 1994; Godfray 1995; Maestripieri 2002). The present simulations can potentially be applied to questions from these areas. For example, questions in life history theory could be investigated by determining effective rules for when to switch from parental investment to having additional offspring. Parental investment theory and parent–offspring conflict involve strategic elements that originate in the conflict over who will invest in offspring and for how long. These components could be added to future models for the

purpose of investigating the nature of biparental care and strategic components of parent–offspring interactions.

#### A role for memory, recognition, and bonding

Our findings suggest that highly social and mobile species with long periods of parental investment cannot effectively use simple proximity maintenance mechanisms to discriminatively transmit benefits to offspring. Mammals are characterized by long periods of parental investment and relatively high mobility (Galef 1981; Kleiman and Malcom 1981), suggesting the need for strategies such as recognition or bonding/attachment to decrease the rates of misdirected and wasted parental investment. It has been suggested that associative learning is a general and viable mechanism for kin discrimination, although ecological and social conditions that lack spatial and associational cues (including female polygamy, communal nesting, brood parasitism, and dispersal) may select for phenotype matching (Holmes and Sherman 1983; Sherman and Holmes 1985).

Although the present model does not specifically address the viability of various kinds of recognition systems (spatial, species, kin, individual), future work will address the effectiveness of such mechanisms in various social and ecological conditions. For example, the effectiveness of offspring caching can be examined by enabling parents to use spatial memory to return to a location in which immobile offspring were placed. Also, the potential benefits of social recognition can be investigated by endowing parents and/or offspring with social memory for one another. Recent simulations have shown that spatial structure can play an important role in the evolution of recognition systems (Axelrod et al. 2004), making this a promising area for future work. Bonding and attachment can be explored by enabling parents and/or offspring to maintain proximity with a particular individual (including the mate in the case of biparental care). Future work along these lines might illuminate the nature of differences in parental behavior and parental cognition among species and the role of ecological factors in shaping selection for various parental investment strategies.

Our findings have implications for understanding the nature of parental investment in various species, suggesting the ecological and social conditions that would favor more complex decision rules underlying parental investment strategies. Although we did not directly explore the viability of more complex systems such as those underlying recognition or attachment, our model demonstrates the limits of this simple recognition system, and in doing so suggests the conditions under which these more complex systems are likely to arise. Future simulations will enable us

to explore the evolution of more complex strategies for parental investment, including both simple recognition systems and more complex bonding and attachment systems. However, it remains important to acknowledge that very simple proximity maintenance rules may be a fundamental component of parental investment in organisms lacking the capacity for complex cognition.

## Appendix 1: Submodels

This section provides additional detail regarding simulation schedule and the subprocesses.

1. *Resources diffuse* between neighboring patches: half of the diffusion amount to patch immediately to right, and other half to patch immediately to left
2. *Parents produce energy*, adding to the resources on the current patch
3. *Agents move*
  - a. Parents move according to mobility, change heading with turn propensity
  - b. Offspring follow benefit approach rule  
If ( $R < R_1$ ), then FD1 else TRN

Where  $R$  = resource level on the present patch,  $R_1$  = the resource level on the patch ahead, FD1 is the movement command, “forward 1,” and TRN is the movement command “turn around” (allowing the organism to repeat this rule facing a different direction in the next time step).

4. *Offspring consume* resources from the current patch

**Acknowledgements** We would like to thank the lab groups of Eduardo Fernandez-Duque, Bruce Ellis and Lee Cronk for helpful comments and suggestions regarding this manuscript. Fernandez-Duque was supported by the Argentinean CONICET and both Aktipis and Fernandez-Duque were supported by the University of Pennsylvania during the analysis of the data and preparation of the manuscript. Aktipis was supported by a NSF Graduate Research Fellowship and National Cancer Institute grants F32CA144331 and R01CA140657. We thank Liz Dong for editorial assistance.

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