

# Using Robots to Understand Social Behavior

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## Abstract

A major challenge in studying social behavior stems from the need to disentangle the behavior of each individual from the resulting collective. One way to overcome this problem is to construct a model of the behavior of an individual, and observe whether combining many such individuals leads to the predicted outcome. This can be achieved by using robots. In this review we discuss the strengths and weaknesses of such an approach for studies of social behavior. We find that robots – whether studied in groups of simulated or physical robots, or used to infiltrate and manipulate groups of living organisms – have important advantages over conventional individual-based models and have contributed much to the study of social behavior. In particular, robots have increased our understanding of self-organization and the evolution of cooperative behavior and communication. However, the resulting findings have not had the desired impact on the biological community. We suggest reasons for why this may be the case, and how the benefits of using robots can be maximized in future research on social behavior.

**Keywords:** Robot, social behavior, collective behavior, Individual-based model (IBM), simulation, model

## 1 Introduction

Social behavior, both in humans and other organisms, has for many years drawn the attention of researchers from a range of fields, as it poses interesting questions from mechanistic and evolutionary viewpoints. Many approaches have been used to study social behavior. These approaches can be classified over a scale of “situatedness”, which we define as the extent to which individuals are embedded in an environment that can be sensed and modified by those individuals (Varela et al., 1991; Clark, 1996). The situatedness spectrum ranges from abstract mathematical models on one end to field work in natural habitats at the other end (Fig. 1).

At one extreme of the situatedness scale, observational or experimental studies performed in the field are useful in that they include the whole complexity of the organisms and their environment. However, while such studies allow one to infer correlations, they rarely permit to unambiguously demonstrate causations, for example in how the behavior of an organism is affected by those of other individuals in the population. The realization of this limitation has led to an active field of experimental studies performed in the laboratory where it is easier to control variables of interest. While these studies have provided important insights into the social behavior of organisms, an important limitation is that it is frequently difficult or impossible to manipulate the behavior of individuals to investigate the response of other group members.

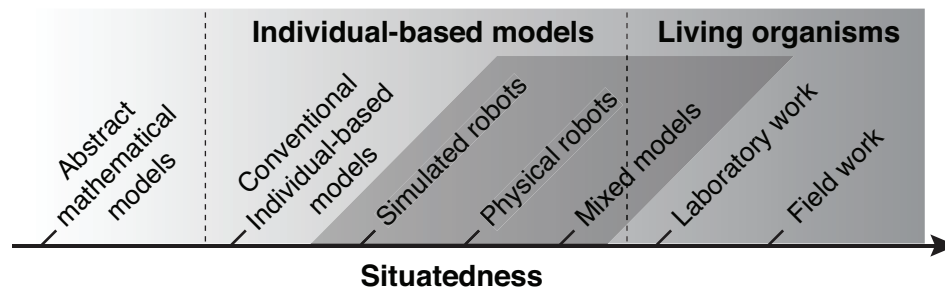


Figure 1. Different approaches to studying social behavior on a scale of situatedness, i.e., the extent to which individuals are embedded in an environment that they can sense and modify. The shaded box represents the robotic models covered in this article.

At the other end of the scale, abstract mathematical models allow one to boil down collective systems to their minimal components and explore the effects of what are considered to be key parameters on their dynamics. While abstract models can make powerful predictions, they generally model populations as a whole thereby neglecting or strongly simplifying the spatial environment, local interactions, life cycle dynamics and phenotypic plasticity (DeAngelis & Mooij, 2005). The realization of the importance of these factors has led to the development of Individual-Based Models (IBMs, a term often used interchangeably with “agent-based models” (Grimm & Railsback, 2005)), where “agents” are modeled individually. Such models allow one to consider individual differences such as age or size and their possible interactions (Judson, 1994; Grimm & Railsback, 2005). These agent-based models have played an important role in explaining social behaviors, and have thus largely been accepted as part of the toolbox for

modeling social systems from small groups to populations and ecosystems (DeAngelis & Mooij, 2005). Agents in these IBMs are typically implemented using computer simulations.

More recently, researchers have resorted to using robots spanning different levels of situatedness, including simulated robots, physical robots, and “mixed models” where physical robots and animals interact (Garnier, 2011; Krause et al., 2011). The aim of this review is to discuss how the use of robots can complement experimental and theoretical studies on social behavior.

Robots have been introduced as a means to study social behavior relatively recently, and the approach has quickly gained momentum (see Garnier (2011) and Krause et al. (2011) for recent reviews). We define a physical robot as “a machine that is able to interact physically with its environment and perform some sequence of behaviors, either autonomously or by remote control” (Krause et al., 2011). Essentially, robotic models of collective behavior are IBMs in which individually-programmed robots interact. As in conventional IBMs, all components of the individual robots are given, making it easier to understand their collective behavior, compared to that of living organisms. However, the main advantage of using robots in a real physical environment over IBMs within a simulated environment is that fewer assumptions need to be made regarding the environmental properties (e.g., spatial constraints, perceptual noise, signal propagation). This is because the laws of physics are included “for free” in robotic models. A direct consequence of this is that experiments using robots are more likely to lead to unexpected and interesting outcomes whenever some property of the physical world that would intuitively not have been included in an abstract environment has an important influence on the resulting collective behavior. This assumes, however, that these physical properties and the resulting behavior are not caused by artifacts that are specific to the robots and do not have parallels in the natural world.

So far, most of the studies involving robots have been conducted by computer scientists and engineers with the effect that much of the published work is unknown to biologists. It is therefore timely to review these studies, assess the extent to which they have contributed to our understanding of social behavior, and outline the most promising directions for future research.

In this article, we classify robotic models used to study social behavior into three categories: (1) simulated robots, where the physical environment and the robots are modeled in computer simulations, (2) physical robots where experiments are conducted with real robots, and (3) mixed models where physical robots interact with living organisms (grey shaded area in Fig. 1).

## **2 Simulated robots**

Simulated robots, here defined as computer simulations of physical robots and their environment, are at an intermediate level on the situatedness scale between conventional IBMs and experiments with physical robots (Fig. 1). While simulated robots may first appear to be equivalent to conventional IBMs, they critically differ in that they are designed to mimic physical robots and their environment, thus forcing the modeler to take constraints in perception, actuation, space and resources into account. Simulated robots have the three following characteristics: (1) they have an extended body (i.e., they occupy space in the world) rather than being a point; (2) they gather information about the environment through sensors that are morphologically located and limited in range and accuracy rather than having an ideal perceptual system that can access global and perfect information; and (3) they move in an extended space with finite distances and resources rather than in mathematical spaces which often have no boundaries and/or infinite resources (see e.g., Fig. 2A). All these factors can significantly affect the outcome of social behaviors that imply physical and perceptual interactions within a confined space. In addition, complete knowledge of the components and functioning of the modeled physical robot and its environment reduces the number of assumptions that need to be made when constructing the simulation, compared to a conventional IBM, which models living organisms that may not be fully understood.

The recent rise in computational power and simulation technology (Waldner, 2008) has led to the development of off-the-shelf robotic simulators that include models of a number of commercially available robots (e.g., Webots™ robot simulator (Michel, 2004)). The degree of realism of these robot simulations varies greatly, ranging from kinematic models of motion and collisions to the more recent physics-based models where friction, masses, elasticity, gravity, and

other physical forces are accurately captured (Bourg, 2002). Typically, the development of robotic simulations is based on systematic experiments, in which the behavior of the physical robots and their simulated counterparts are compared until the latter prove to be reliable substitutes for the former (e.g., Mondada et al. (2004)). This systematic approach ensures that the assumptions and design decisions in constructing a given model are more explicit, rigorous and less likely to be chosen for convenience.

Compared to conventional IBMs, the increase in model situatedness reduces the risk of overlooking important properties of the physical environment on social behavior. For example, in a study on the evolution of communication using simulated robots, Mitri et al. (2009) found that the clustering of foraging robots (Fig. 2B) around a food source provided inadvertent information to other robots on food location thus greatly influencing the selection pressure on communicative strategies. The resulting strategies – which depended on the existence of inadvertent information – provided an explanation for the high variability in communicative strategies in many animal species that had been difficult to explain prior to this study. Models using simulated robots thus provide an advantage over conventional IBMs in scenarios where spatial and visual effects are likely to influence social behavior.

Physics-based robotic simulations have an important advantage over the use of physical robots because they allow one to conduct numerous experiments with many individuals. This is an important issue if one wants to conduct experimental evolution over hundreds of generations. For example, an experiment on the evolution of communication where 100 groups of 10 foraging robots each had to forage for 20 minutes during each of 500 generations, lasted less than a week with a cluster of 40 computers in simulation (Mitri et al., 2009). Assuming no interruption to the experiments, the total run-time would have been almost two years for each of the three experimental treatments if the experiments would have been conducted with physical robots. Interestingly, it was possible to implement the evolved behavior in physical robots at the end of the 500 generations of selection to confirm the robustness of the behavior observed in the simulations (Fig. 2B).

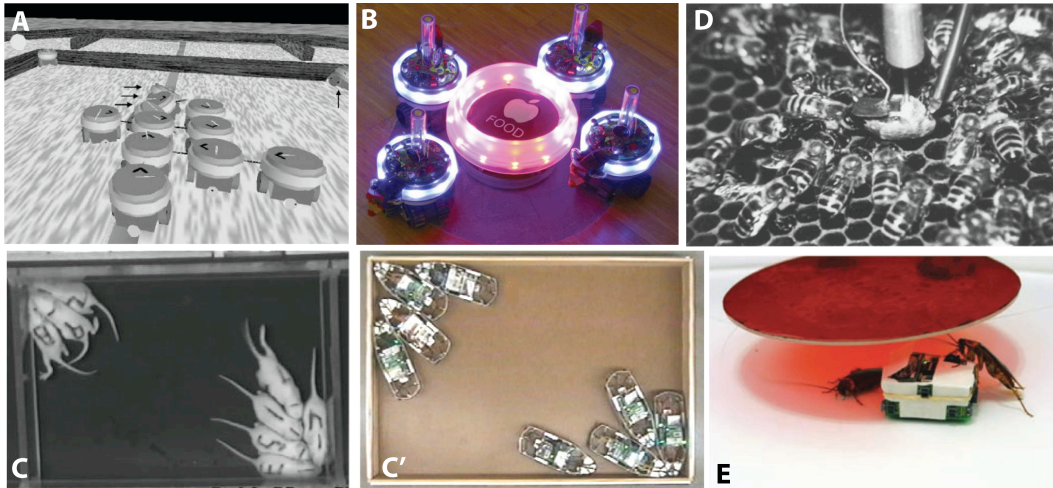


Figure 2. Robots used to study social behavior. A. Simulated robots to study coordination of collective behavior (Baldassarre et al., 2006). B. Foraging robots used to study the evolution of communication (Mitri et al., 2009). C. Modeling rat pup aggregation behavior using robots (C') (May et al., 2006). D. Robotic bee to test hypotheses on honeybee dance language (Michelsen et al., 1992). E. Robots used to explore decision-making in cockroaches (Halloy et al., 2007).

### 3 Physical robots

Compared to simulated robots, studies with physical robots implicitly include properties of a physical environment. They therefore provide a particularly valuable tool when one or more of these properties are expected to be important in influencing social interactions. This is nicely illustrated by two studies on the aggregation behavior of the German cockroach *Blattella germanica*. Using an IBM based on empirically measured values, Jeanson et al. (2005) attempted to reproduce the behavior of the cockroaches. Although there was a qualitative agreement between simulations and empirical data, the IBM led to larger aggregates than those formed by the cockroaches. A follow-up study with physical robots provided a better match with the empirical data (Garnier et al., 2008). An analysis of the results revealed that this was because Jeanson et al. (2005) had not included the possibility for the software agents to hide behind each other. The software agents in the IBM were thus able to perceive many more individuals in a cluster, resulting in larger and more stable aggregates than with robots and real cockroaches (Garnier et al., 2008).

Another property of robotic systems that is rarely taken into account in conventional IBMs are physical interactions between individuals that influence each other's movement. The role of such

physical interactions was demonstrated in a study where a swarm of small ant-like robots was programmed to collect objects scattered in an arena (Krieger et al., 2000). These experiments revealed that foraging efficiency was lower in larger groups because there was more interference among robots than in smaller groups. This study thus provided a possible explanation for the observation that per capita productivity decreases with group size in many social insects.

Friction and body shape were found to also be crucial to collective behavior in a study with rat-like robots aimed at mimicking how new-born rat pups form aggregations in small spaces (May et al., 2006). When setting up a baseline algorithm where robots were programmed to move randomly, the authors found that this random algorithm best fit the collective behavior observed in the pups. Although it was commonly thought that new-born rat pups have an instinctive attraction to objects and other rat pups (Schank et al., 2004), the study by May et al. provided a novel testable hypothesis whereby pups may simply be moving randomly and, as a result of their body shape and the friction between individuals, end up huddled in tight aggregations (see Fig. 2C and C').

## **4 Mixed models**

A particularly powerful application of physical robots to the study of social behavior is the possibility of infiltrating animal societies with physical robots. Such mixed models allow the experimenter to gain insights into the animals' behavioral codes. While the use of dummies and decoys to manipulate and study animal behavior dates back to ethologists of the 1930s and 40s (Tinbergen, 1948), the use of robots as dummies allows the experimenter to program more sophisticated behavioral sequences and to conduct closed-loop experiments where a robot can react to sensory input triggered by an animal. For example, robots were used to test how groups of cockroaches select a common shelter (Halloy et al., 2007). The decision-making process was studied by covering four robots with filter paper carrying the cockroaches' odor and mixing them with a group of 12 cockroaches. While groups of 16 cockroaches showed a preference for darker shelters, the authors found that this collective decision could be altered if the four robots were programmed to choose the less-preferred brighter shelters. From these experiments, the authors

concluded that a minority of individuals could strongly influence the groups' decisions (see Fig. 2E), thus supporting conclusions drawn by previous studies using IBMs (Couzin et al., 2005; Huse et al., 2002).

Similarly, Michelsen et al. (1992) used a robotic bee to test a long-standing controversy regarding the honeybee dance language. The use of robots permitted the authors to disentangle the roles of several components of the waggle dance on the bees' foraging behavior, thus confirming that the waggle dance conveys abstract information on distance and direction of a source of food (Fig. 2D).

The robots used in mixed models, rather than being models in their own right, can be regarded as experimental tools used to interact with and manipulate real organisms, and therefore do not fit as cleanly into the scale of situatedness as the simulated and physical robots discussed above. Nevertheless, they have played an important and increasing role in the study of social behavior at the intersection of robotics and biology, as reviewed by Krause et al. (2011). Mixed models and the use of "cyborgs" where animal behavior is manipulated by electronic devices have already allowed to push the boundaries of behavioral research and there are a number of exciting future research avenues in wildlife management, the exploration of imitation and social learning, the decoupling of morphology and behavior and the study of social networks (Krause et al., 2011).

## **5 Robots have advanced our understanding of social behavior**

The study of social behavior has centered around understanding apparently sophisticated and complicated collective behavior both from a mechanistic and evolutionary viewpoint. A number of important questions relating to these viewpoints have been addressed using physical robots, simulated robots or mixed models. We have compiled these into a list of 52 studies, some of which have generated novel and testable hypotheses (Table 1).

One such question is how individuals coordinate their efforts to achieve a common goal (Couzin, 2009). Experiments using both physical and simulated robots have been instrumental in showing that efficient self-organization processes can occur even with little sensory information



(Melhuish et al., 2006; Holland & Melhuish, 1999; Baldassarre et al., 2006; Groß et al., 2008). For example, in experiments by Groß et al. (2008), simple physical robots following identical local rules were required to retrieve a heavy “prey” and transport it to a “nest” – a relatively complex task that could not be conducted by any individual robot alone. The authors found that the robots self-organized into groups performing different tasks (e.g., forming a path from the object to the nest), illustrating that division of labor can take place simply due to differences in local perception, in the absence of inter-individual differences and individual recognition. Self-organization has also been shown to take place without any communication (Kube & Bonabeau, 2000) or memory (Holland & Melhuish, 1999). Both of these studies, in which physical robots were used, have generated predictions that can be tested experimentally, for example to determine which of a number of algorithms is used by foraging ants. Other mechanisms, such as the use of simple oscillatory processes in neural networks, have been shown to lead to self-organized, synchronized light emission patterns in groups of physical robots interacting with each other at close ranges, perhaps analogous to synchronized firefly light production (Wischmann & Pasemann, 2006; Wischmann et al., 2006). Similarly, the production of rhythmic signals can evolve as a means to allow simulated robots to coordinate group behaviors, suggesting that turn-taking in duetting birds may serve a similar purpose (Di Paolo, 2000).

While the behavior of robots in these studies was mostly pre-programmed, other studies have investigated how social behavior can evolve by the mere effect of mutation and selection (Floreano & Keller, 2010). For example, Nolfi and Floreano (1998) have shown how competitive co-evolution between populations of predator and prey robots can drive the evolution of novel pursuit or escape strategies that were not observed when only one of the two populations was evolving. The study has also suggested that co-evolving organisms may evolve to specialize to their current opponents, a hypothesis which was later tested in co-evolving populations of bacteria and parasitic bacteriophages (Buckling & Rainey, 2002). Experimental evolution has also been used to investigate the role of genetic relatedness on the evolution of cooperative behavior. By allowing simulated robots to evolve in groups with different levels of relatedness, Waibel et al. (2011) were able to conduct a quantitative test of Hamilton’s rule (Hamilton, 1964)

and demonstrate that it was possible to exactly predict the minimum relatedness required for altruism to evolve when the costs and benefits of altruistic behaviors could be controlled.

Table 1. The articles in this table were chosen because they report on research using simulated robots, physical robots or mixed models, and explicitly state that they aim to understand social behavior in living organisms. One representative article was chosen when numerous articles had similar conclusions. Citations in bold have generated new, testable hypotheses.

	Simulated robots	Physical robots	Mixed models
Hypothesis-driven	Floreano et al., 2007 Marocco et al., 2003 <b>Melhuish et al., 2006</b> Mitri et al., 2009 Waibel, 2011 <b>Wischmann et al., 2012</b>	Floreano et al., 2007 Garnier et al., 2008 Garnier et al., 2009 Groß et al., 2008 <b>May et al., 2006</b> <b>Melhuish et al., 2006</b>	Faria et al., 2010 <b>Fernández-Juricic et al., 2006</b> <b>Göth &amp; Evans, 2004</b> Halloy et al., 2007 <b>Martins et al., 2005</b> Michelsen et al., 1992 <b>Ord &amp; Stamps, 2008</b> Partan et al., 2009 <b>Patricelli et al., 2002</b> Patricelli et al., 2006 <b>Reaney et al., 2008</b> Reaney, 2009 Rundus et al., 2007 Sumpter et al., 2008 Taylor et al., 2008
Exploratory	Baldassarre et al., 2006 <b>Di Paolo, 2000</b> Labella et al., 2006 Marocco et al., 2003 Marocco & Nolfi, 2006 Mataric, 1993 Mitri et al., 2009 Quinn, 2001	Belpaeme & Birk, 1997 Birk & Wiernik, 2002 Garnier et al., 2007 <b>Holland &amp; Melhuish, 1999</b> Krieger & Billeter, 2000 <b>Krieger et al., 2000</b> <b>Kube &amp; Bonabeau, 2000</b> Labella et al., 2006 Mataric, 1993 McFarland, 1994 <b>Nolfi &amp; Floreano, 1998</b> Rubenstein et al., 2009 Schmolke & Mallot, 2002 Steels & Vogt, 1997 Steels, 1998 Vogt, 2000 Wischmann & Pasemann, 2006 Wischmann et al., 2006	Böhlen, 1999 Gribovskiy et al., 2010 Kubinyi et al., 2004 Landgraf et al., 2008 Takanishi et al., 1998

Several other studies have also focused on the evolution of communicative behavior, a question that has been difficult to address using other experimental methods, because many forms of animal communication evolve over large time-scales and leave no fossil record. For example, Quinn (2001) demonstrated that signals between two simulated robots can evolve from sensors that were originally used for obstacle avoidance rather than communication, thus suggesting a mechanism for the evolution of natural communication channels. Other studies have investigated

how group structure may affect the likelihood to cooperate and communicate. Experimental evolution in groups of robots differing in genetic relatedness revealed that honest communication can evolve in simulated robots when communicating individuals are highly related (Floreano et al., 2007), while unrelated individuals evolve to suppress information transfer to other group members (Mitri et al., 2009, 2011). Wischmann et al. (2012) have similarly used experimental evolution in robot groups to explain how variations in communication systems can occur as a result of the order in which novel phenotypic traits are acquired in independently evolving populations. The study also demonstrates a trade-off between communication efficiency and robustness. Studying communicative behavior in animal groups has also benefited from the use of robots. Mixed models have succeeded in revealing the importance of communication in some group behaviors (Fernández-Juricic et al., 2006; Reaney et al., 2008), disentangling the different components of signaling systems (Martins et al., 2005; Göth & Evans, 2004; Patricelli et al., 2002; Michelsen et al., 1992; Rundus et al., 2007), and showing how these components interact to increase communication efficiency in noisy environments (Partan et al., 2009; Taylor et al., 2008; Ord & Stamps, 2008).

Wheeled and humanoid robots have similarly been used to investigate human language and explore how continuous perceptual data can be mapped onto discrete “words” or symbols (Harnad, 1990). These studies have established that interacting with the environment and with other simulated or physical robots can lead to categorization of perceptual data (Marocco et al., 2003; Marocco & Nolfi, 2006), the formation of “vocabularies” (Steels & Vogt, 1997; Vogt, 2000) and even simple forms of syntax (Steels, 1998). Because the perceptual data that a robot is exposed to, as opposed to a simulated individual, is similar in richness to information collected by a living organism, the use of robots has proven to be a valuable tool in understanding how living organisms categorize information and map it onto symbols. For example, a robot may approach the same object from different sides, but will still need to recognize the object in order to assign a name to it (Loetzsch & Spranger, 2010).

## **6 Evaluating robotic models**

Although robotic models have been useful in addressing a variety of issues on social behavior, these studies are only infrequently integrated into the biological literature. Subsequently, hardly any of the hypotheses generated by robotic models outlined above have been tested using living organisms. There are at least two main reasons for this. The first is that many of these studies are published in computer science or artificial life journals that are infrequently read by the biological community. The second reason is that many of these studies do not use a “hypothesis-driven” approach (Table 1, see also “strong inference” (Platt, 1964)). Currently, much of the work in biology consists of hypothesis-driven experiments with researchers designing experiments to test a specific hypothesis. So far only a minority of the experiments conducted with robotic models are of this type. Most have been “exploratory” with a model being constructed to explore whether the implicit inclusion of the robots’ physical properties will reveal novel aspects concerning the collective behavior in question. While such exploratory studies may be less constrained in how they approach a given problem, and thus may uncover unexpected patterns, they carry the risk of not answering a particular question. Furthermore, because these studies are not designed to test a specific hypothesis, the results are usually less convincing and it may be more difficult for a biological audience to draw parallels and apply these findings to their own work. In hypothesis-driven experiments, on the other hand, controlled manipulations make it easier to understand causal mechanisms, and thus to link the model results to similar natural phenomena.

Since the birth of the scientific method, scientists and philosophers have been debating the most promising and efficient methods to improve our understanding of nature. In the 17th century, Francis Bacon discussed this point, asking whether researchers should collect data in an exploratory manner “without premature reflection or any great subtlety” (Bacon, 1620). These observations could then be used to construct scientific theories. In a recent article, Franklin (2005) argued that scientists tend to resort to such exploratory methods when a new tool becomes available for data collection, and when that tool allows for the collection of vast amounts of data. This allows them to map out new scientific territory. Consistent with Franklin’s analysis, researchers studying social behavior with robots have initially mostly conducted exploratory studies to determine whether the embodiment of agents in a physical world leads to

surprising outcomes increasing our understanding of social behavior. More recently, the trend appears to have shifted towards a higher proportion of hypothesis-driven studies (see Table 1 and Fig. 3).

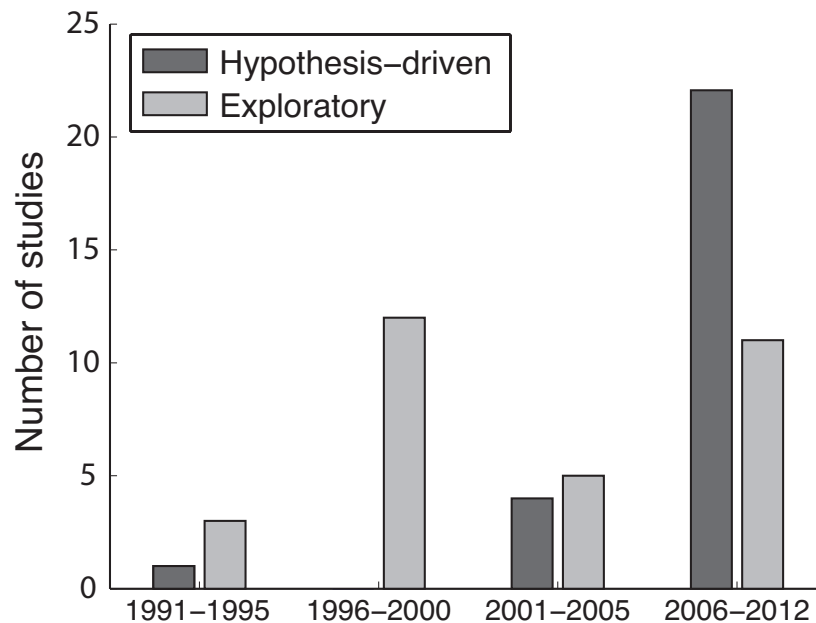


Figure 3. Figure 3: Histogram of the number of hypothesis-driven versus exploratory studies over the last 2 decades.

The shift from exploratory to hypothesis-driven experiments is to a large extent due to a recent increase in studies using mixed models. This is perhaps because mixed models are often designed by researchers working on a living system and who use robots to address a specific question that could not be answered otherwise. The robots thus often serve as an experimental tool to systematically vary parameters and test for their effects. These hypothesis-driven studies also appear to have led to a greater number of novel hypotheses that can be tested in a biological context than exploratory studies (see highlighted studies in Table 1).

Another reason why biologists might be reluctant to utilize results from robotic studies is that it is not always clear how the behavioral code of the robot is implemented and whether this implementation is biologically relevant. One way to overcome this problem would be for modelers to explicitly and objectively define the behavioral code that is used by a robot in order

to provide the reader with sufficient information to evaluate the results of a study and its parallels in biological organisms.

## **7 Summary and future directions**

Our review of the literature shows that robots have contributed to our understanding of social behavior, both through exploratory studies, whereby the complexity of the robots' social behavior in a physical environment is used to inspire further empirical studies, and through hypothesis-driven experiments. Robots represent a modeling niche by occupying the situatedness space between agent-based models and real organisms. Because one has full access to the sensors and actuators of a robot, it is easier to control and understand than a living organism. At the same time, the increase in situatedness compared to agent-based computer simulations provides an advantage whenever certain physical features of the real world are expected to influence social behavior or when the question is specifically about the influence of certain physical properties that can be considered with the robot. The examples listed in this review illustrate how visual and spatial effects can influence aggregation, search or communicative behaviors (Jeanson et al., 2005; Garnier et al., 2008; Mitri et al., 2009), and how friction and collisions between individuals can play an important role in collective foraging (Krieger et al., 2000; Krieger & Billeter, 2000; Kube & Bonabeau, 2000; Waibel et al., 2011) and clustering behaviors (Holland & Melhuish, 1999; May et al., 2006; Melhuish et al., 2006).

However, the benefit of using robotic models rather than conventional IBMs depends on the particular question one is addressing. Ideally, the chosen model will be similar enough to the real system to include all the factors of interest and relevance, yet simple enough to allow control over the various parameters of the model and adequate analysis of the results. Consequently, robots are not always the tool of choice. Rather, they should be considered only when the properties of a robot, physical or simulated, are likely to influence the outcome of a particular experiment. Furthermore, if the conclusions of a study using robots are found to be independent of any such physical properties, one can then reduce the complexity of the study to a simpler model that captures the natural observation more concisely. A further limitation of using robots

is that some observations may be due to artifacts that are particular to the robots, and may not correspond to any natural phenomena. This problem can be avoided by conducting a detailed analysis of the mechanisms responsible for an observed behavior, and making concrete comparisons with empirical biological data (Webb, 2009).

Nevertheless, we believe that there is much potential for the use of robots that has yet to be explored. For example, there is much discussion on how individual and kin recognition affect decisions made within a collective (Sheehan & Tibbetts, 2008; Paterson & Hurst, 2009; Nehring et al., 2011). Because such recognition is based on noisy sensory information, distinguishing between individuals may be difficult both for animals and robots that must solve the task in the physical world. It would be interesting to see whether similarities in sensory perception between animals and robots – compared to abstract agents – may give some insights into the role of peer recognition in collective decision-making. In robots and animals one might, for example, expect a certain level of error in recognizing others that may influence the social dynamics of the group.

Another potential use of robots is to study the interplay between mechanistic properties that are highly dependent on physical factors, and effects arising over evolutionary time. Mayr (1961) and Tinbergen (1963) were perhaps the first to argue for the synergistic benefits of a complementary approach addressing both proximate (mechanistic) and ultimate (evolutionary) causes. As has been discussed in this review, the use of evolutionary robotics has been instrumental in exploring such questions in groups of robots, and has resulted in important contributions to our understanding of the evolution of social behavior, thus highlighting the strength of robotic models. Such a complementary approach could be similarly applied with mixed models to study the interplay between behavioral and evolutionary processes. A nice illustration of this idea is provided by a study where blue jays searched for digital moths on computer monitors (Bond & Kamil, 2002). The digital moths that were not pecked by the birds survived to subsequent generations, thus allowing to investigate how selection shapes phenotypic properties of moths. Although this study did not involve robots, it may inspire similar studies using mixed models where the robots' controllers or morphology can evolve in parallel with organisms with a short generation time. Such an approach provides a unique opportunity to investigate how social interactions can affect the evolutionary pathway of organisms and the

evolution of complex social systems (Rosenthal & Evans, 1998; D'Eath, 1998; Baldauf et al., 2008; Moiseff & Copeland, 2010).

Finally, it is important to note that physical robots have become cheaper and simulations easier to design and perform. Robotic research platforms have also become available, such as the Symbion system, which consists of hundreds of miniature robots that can be used for evolutionary and collective experiments (Kernbach et al., 2008). This should contribute to making robotic systems more frequently used to address biological questions that are difficult or impossible to address with real organisms.

## **8 Conclusions**

1. Robots have made important contributions to the study of self-organization, communication and the evolution of competitive and cooperative behavior.
2. Both exploratory and hypothesis-driven studies using robots have generated novel hypotheses that can be tested using living organisms. However, the more recent shift toward hypothesis-driven studies is likely to make these findings more accessible to the biological community.
3. The choice of modeling tool depends on the question of interest and can be selected from different levels of “situatedness”. The model should be similar enough to the real system being studied to include all components that are relevant to generating the observed empirical data, yet simple enough to be amenable to detailed analysis and understanding.
4. Robots are useful when properties of the physical environment (e.g., visual and spatial effects, friction and collisions) are likely to influence the outcome of the social behavior.

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