

Interactive robots in experimental biology

Jens Krause^{1,2}, Alan F.T. Winfield³ and Jean-Louis Deneubourg⁴

- ¹ Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Department of Biology and Ecology of Fishes, 12587 Berlin, Germany
- ² Humboldt-University of Berlin, Department for Crop and Animal Sciences, Philippstrasse 13, 10115 Berlin, Germany
- ³ Bristol Robotics Laboratory, University of the West of England, Coldharbour Lane, Bristol, UK, BS16 1QY
- ⁴ Unit of Social Ecology, Campus Plaine CP 231, Université libre de Bruxelles, Bd du Triomphe, B-1050 Brussels, Belgium

Interactive robots have the potential to revolutionise the study of social behaviour because they provide several methodological advances. In interactions with live animals, the behaviour of robots can be standardised, morphology and behaviour can be decoupled (so that different morphologies and behavioural strategies can be combined), behaviour can be manipulated in complex interaction sequences and models of behaviour can be embodied by the robot and thereby be tested. Furthermore, robots can be used as demonstrators in experiments on social learning. As we discuss here, the opportunities that robots create for new experimental approaches have far-reaching consequences for research in fields such as mate choice, cooperation, social learning, personality studies and collective behaviour.

Introduction to interactive robots

Tinbergen [1] demonstrated that, in some species of fish, birds and butterflies, only simple stimuli are required to elicit territorial or mating behaviour that is normally only shown in response to male and female conspecifics. Insights into the mechanisms of social recognition coupled with technological advances suggest that robots (see Glossary) can be developed for use in behavioural research to simulate con- and heterospecific behaviour. For the purposes of this review, we define a robot as a machine that is able to interact physically with its environment and perform some sequence of behaviours, either autonomously or by remote control. In recent years, there has been a transition from robots that, once set in motion, 'blindly' follow a particular programme, to ones that can interact with their environment, learn and even adapt [2-5]. This creates many opportunities for the use of robots in experimental biology, particularly when investigating social behaviour.

One of the main challenges when investigating social behaviour is that the behaviour of individuals is dependent on that of their interaction partners. It is possible to infer certain rules or strategies from behavioural observations but unless one can manipulate the behaviour of individuals, this approach remains largely descriptive. One way to manipulate behaviour is to create robots that are accepted as con- or heterospecifics and that can be programmed to carry out specific behavioural patterns. A related approach that serves the same purpose (i.e. of getting control over

the behaviour of one or more individuals in a group or population) is to fit a live animal with interactive technology so that one animal in a group is effectively controlled as the 'robot' that interacts with its conspecifics. A brief overview of robots and interactive technologies is provided in Box 1.

Here, we give an overview of interactive robotics for use in experimental biology, focusing on social behaviour. This approach has been successfully used across the animal kingdom ranging from studies on social insects [6,7] and cockroaches [4] to ones on fish [8], birds [9] and mammals, including humans [10–13]. Previous reviews on robots in biological research [14–17] were less focussed on the interactive component, which is a recent technological development and has become an important component of studies on collective behaviour [4,18–21]. We identify important novel biological research questions that can be answered with the help of interactive robots and outline new directions for future developments in machine–animal interactions.

Interactive technologies

Robots and computer animations

Robots are not the only way to create interactions with live animals. Animations in which virtual animals on a computer screen display realistic behaviours and interact with live animals have become an important tool for investigating

Glossary

Animal personality: individual consistency in behaviour across time and/or contexts.

Autonomous robot: a robot with sensory input, decision-making capabilities and behavioural output.

Cognitive ability: information-processing ability in connection with problem solving.

Collective behaviour: the field of collective behaviour investigates the emergence of group-level properties from interactions among individuals.

Consensus decision: agreement among group members on one course of cotions.

Cyborg: an organism with both biological and electronic parts.

Quorum: a threshold number of individuals that, once reached, will lead to a behaviour or action for the whole group (see also consensus decision).

Robot: a machine that is able to interact physically with its environment and perform some sequence of behaviours, either autonomously or by remote control.

Self-organisation: individuals follow local behavioural rules, resulting in organised behaviour by the whole group without the need for global control. **Swarm intelligence**: collective behaviours, in both natural and artificial systems of multiple agents, that exhibit group-level cognition.

Swarm robotics: the design and engineering of artificial robot swarms based on the principles of swarm intelligence.

Box 1. Overview of interactive technologies

Autonomous robot

An autonomous robot is a robot with sensory input that is capable of determining its next action (both what action to take and when to take it) without human intervention. It is autonomous in the sense that it can make and execute decisions based on its own assessment of its environment. Autonomous robots are capable of interaction with live animals without human guidance. An example of this type of robot is the cockroach-robot (Figure 1, main text), which was used to investigate communal shelter selection (see section in main text on Robots in behavioural experiments).

Cyborg

A cyborg is an organism with both biological and electronic parts; the latter enable direct control of an animal by manipulating its nervous system. This control can be used for manipulating the locomotion of an animal or its social interaction with conspecifics. The control of flight performance in beetles provides an example of this novel approach to controlling animal behaviour (Box 2).

Remote-controlled robot

A remote-controlled robot is one whose behaviour is controlled externally (in contrast to an autonomous robot whose control centre is inside the robot itself) by a human observer or a computer outside the robot. The robotic fish (Box 3) and the robotic bee [7] are recent examples of this kind of approach.

Smart collars

A smart collar is a device that can be mounted on an animal (usually in the form of a collar around the neck), which provides negative feedback if the animal enters an area where it is not supposed to go. The negative feedback consists of weak electric shocks or repellent noises and is triggered by either a GPS unit inside the collar that locates position of the animal, or an underground wire. This approach is used to retain domestic animals within certain boundaries without the use of fences (see section in main text on Interactive technologies).

animal behaviour [22-24]. This approach has provided many new insights, particularly in the areas of sexual selection and prev recognition [23]. Some of the major advantages of using virtual animals (compared with using real ones) are that it becomes possible to standardise the behaviour of display individuals in choice experiments and to decouple behaviour and morphology. For example, this approach made it possible to identify the role of male ornaments in mate choice of female swordtail fish (Xiphophorus *helleri*) [25]. The use of animation enabled the presentation of the same behaviour by males with a sword-tail versus ones without a sword-tail but with an enlarged body to compensate for loss of surface area. This approach decoupled morphology and behaviour, and demonstrated that the sword does not simply help to increase perception of male size in females.

However, animations with virtual animals also have many limitations because they are largely restricted to the use of visual stimuli in two dimensions. Many animal interactions require other, or additional, sensory input [e.g. fish species can usually sense the presence of conspecifics through the lateral line (via mechanical stimuli) and most species of social insects require olfactory stimuli for social recognition] and occur in three dimensions. They require the physical presence of a con- or heterospecific to fight, mate or cooperate with and these types of interaction, by their very nature, cannot be established with a virtual partner and require a robot.

Although robots can provide solutions to some of the issues connected with virtual animals, they also have potential problems of their own. Developing robots that are accepted as conspecifics might not be equally straightforward in different species (depending on which sensory channels are used for social recognition, the size of the species and its cognitive abilities, to name but a few factors) and the difficulty of implementing movements and responses varies considerably. Building robots can also be time consuming and, in some cases, expensive. It also often requires collaboration with scientists in other disciplines. Despite these potential problems, there are, in principle, no limits to how much a robot can be made to look like a con-or heterospecific in terms of its behaviour and morphology.

Smart collars and cyborgs

New devices, such as electronic collars, make it possible to get control over some aspects of the behaviour of animals and therefore enable behavioural manipulations without investing substantial effort to create an animation or build a robot. These devices were originally developed for domestic animals, which can be fitted with a 'smart' collar that produces an adverse stimulus (sound, odour or mild electric shock) if the animal comes too close to the boundary of its designated area where a wire has been buried that communicates with the collar. This technology is already commercially available for domestic dogs. However, for larger scale use in cattle herding, the collar usually contains a global positioning system (GPS) unit that can determine the location of the animal and that is more flexible and cost effective. An example of such work is the virtual fence project, which promotes the spatial control of livestock by means of smart collars instead of fences [26–28]. Additionally, by making use of social hierarchies and collective behaviour, only a small fraction of the total herd usually needs to be equipped [18,29,30].

However, although it is possible to exert some influence on the behaviour of animals in this way (i.e. they can be maintained in a certain area), it does not produce the kind of fine control that a robot provides. The strength of the response of the animal and its movement details cannot be reliably controlled with a collar and are left to chance. This means that if the same individual is given the same collar stimulus repeatedly, it might still produce a variable behavioural output. In addition, there is often considerable interindividual variation in response to the collar stimuli [27]. An alternative to smart collars is the work on 'cyborgs' ([31–33], Box 2).

Making robots interactive

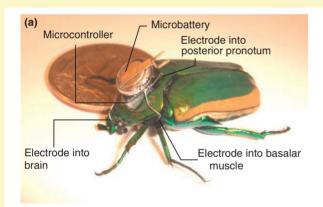
There are several common, basic requirements that must be fulfilled if interaction with live animals is to be possible. The behaviour of live animals needs to be monitored (e.g. through direct observation or an automated camera system) to provide the sensory basis for a response by the agent (virtual animal or robot). This sensory information is used to make a decision (usually by a human observer or a computer) over how the agent should respond in the next time step. Depending on what the live animal does next, this can potentially lead to a chain of interactions between the animal and agent. Some researchers use a

Box 2. Cyborg insects

A novel way to control animal behaviour is to stimulate the neural system of an organism directly. An impressive example of such a 'cyborg approach' is the remote control of insect flight [31–33]. A radio-equipped microcontroller emits pulses via electrodes to the brain and selected muscle groups. Reliable control of flight initiation, cessation, elevation and direction has been possible. Two species of beetle, *Cotinis texana* and *Mecynorrhina torquata*, were used, both of which were strong enough to carry the equipment during flight (Figure I).

Costs and benefits

The Cyborg approach opens new means of controlling locomotion in insects that could be used in many different ways to manipulate interactions among con- or heterospecifics. However, some interindividual variation in responsiveness was observed and the approach is restricted to species that are strong enough to carry the equipment. Both restrictions could be overcome as smaller and more sophisticated technology becomes available. There are also ethical considerations to be taken into account, especially if this approach were to be applied to vertebrates. Furthermore, in the case of more complex social behaviours, it might be necessary to show that the behaviour has not become artificial in any way. For example, a behavioural response might be produced that is normally not observed in a given context.



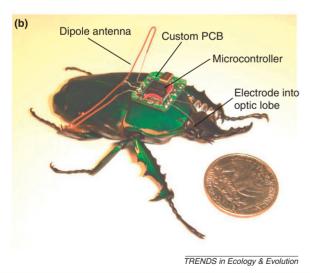


Figure I. Cotinis texana (a) and Mecynorrhina torquata (b) with the equipment for flight control fitted. PCB (printed circuit board) was only used for M. torquata.

simple remote-control system to initiate a response in the robot when they want to create an interaction between a live animal and a robot [9]. This means the first two steps regarding sensory input and decision-making (discussed above) are operated by a human observer. This approach has the disadvantage that much is left to the judgement of the scientist operating the robot. More sophisticated systems give the robot sensory input, a control system and behavioural output so that it can make its own (standardised) decisions as to when and how to interact [4]. This approach can result in an autonomous robot where the animal and the robot interact without intervention from an observer [4]. As an alternative, the control system can be externalised to enable the experimenter to change the course of an interaction between robot and animal at any point (Box 3). For example, the experimenter could load a new interaction sequence if the context required it.

Furthermore, for the analysis of robot–animal interactions and the operation of remote-controlled robots, two- or three-dimensional tracking of robot and animal(s) is vital and is usually done via digital video cameras connected to a computer. Although great advances have been made in using pattern recognition and tracking in recent years [34], fully automated tracking of multiple objects (robots and/or animals) can still be surprisingly problematic under experimental conditions.

Robots in behavioural experiments

Interactive robots have the potential to revolutionise the way in which experimental work with animals is performed because they provide several important methodological advances.

Manipulation of interaction sequences

Interactive robots enable researchers to investigate entire interaction sequences where formerly scientists could only provide an animal with a single stimulus and then wait for a response. Many, if not most, animal interactions involve behavioural sequences that were previously difficult to test experimentally in a standardised way. Particularly relevant behavioural contexts that can involve lengthy interaction sequences include cooperation, courtship and agonistic behaviours, and the fast-growing research area of collective behaviour.

Communal roosting is a wide-spread behaviour but little is known about how individuals agree on a location. To investigate the mechanisms of communal shelter seeking in cockroaches (*Periplaneta americana*), robots were created that behaved in a similar way to cockroaches and that were accepted as conspecifics (based on their odour) by the cockroaches ([4]; Figure 1). The robots were autonomous and capable of recognising the shelters and the walls of the arena, and of interacting with the cockroaches. The cockroaches preferred the darker of two shelters but in the presence of cockroach robots that 'preferred' the lighter shelter, they could be made to accept the lighter one more often than they normally would. The robots, despite their preference for the lighter shelter, occasionally followed the cockroaches and occupied the darker one. The experiments showed that the eventual outcome (adoption of the dark or light shelter) was a result of a complex interaction between robots and cockroaches. The non-linear nature of the decision-making process could result in either the cockroaches or the robots taking charge in the shelter selection process.

Box 3. Robofish

Faria et al. [8] developed a robotic fish (Figure I) whereby a dummy is mounted on a thin Plexiglas rod fixed to a flat magnet and guided by a robotic arm under the tank that carries an electromagnet. The robotic arm is controlled via a computer so that the movements of the dummy can be programmed. When a digital video camera is positioned over the tank, information on the relative position of the dummy to live fish and their behaviour can be processed by a computer and behavioural responses of the dummy can be initiated via the robotic arm. This would close the feedback loop and enable interactions with live fish. If small remote-controlled devices instead of a robotic arm are used under the tank to carry electromagnets, then multiple dummies can be controlled and moved simultaneously.

Costs and benefits

The advantage of this system over autonomous robots lies in the fact that the control system is separated from the dummy. This means that the same control system can now be used for all kinds of dummy, which can be produced in large number at low cost and quickly exchanged. This approach is not limited to fish or aquatic systems and could be adopted for most organisms that are small enough so that experiments can fit into an arena of a few square metres. The system is relatively low cost because it only requires a standard computer, several electromotors and controllers. Potential costs are that this system can only be used in the laboratory (outdoor use is not necessarily straight forward with autonomous robots either) and the dummies have a range that is restricted to that of the two-dimensional arena that is monitored by the camera and serviced by the robotic arm.

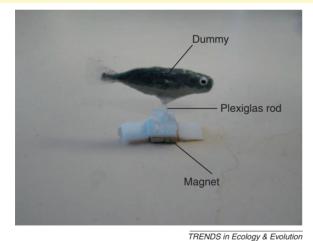


Figure I. The robotic fish was mounted on a plexiglass rod which was attached

to a white plastic plate which was used for stabilisation on the tank floor.

Selecting a common shelter (from two alternatives) involved many interactions between cockroaches and robots over an extended time period.

Another promising area in which interaction sequences are particularly important is that of mating displays where a mixture of different signals are used and where the actions of the sexes are highly interdependent. Interactive robots could provide opportunities for simulating different male courtship behaviours to evaluate their effect on females and, likewise, different female responses to male courtship [35]. An example is the elegant work by Patricelli et al. [9,36] in which robotic female bowerbirds (Ptilonor-hynchus violaceus) were used to investigate male courtship behaviour. A startle response in females significantly re-

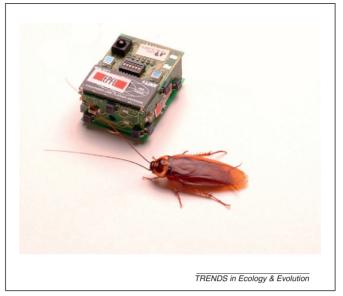


Figure 1. Interactive autonomous robot that can interact with cockroaches. It carries the olfactory signature of a cockroach and, therefore, is treated as a conspecific by cockroaches.

duced the courtship intensity in males [35]. Patricelli *et al.* used a technique by which the researcher triggered the response of the robotic female by remote control from a hide when the bowerbird male began courtship. Therefore, the timing of the response was determined by the experimenter and depended on his or her accuracy of judgment. Given that the experimenter's perspective (from a hide) is likely to be different from that of the female robot, which has a more direct and localised view, it would be an interesting challenge to provide the robot with local sensors that enable it to trigger its own startle behaviour in response to details of the male courtship display that might not even be perceptible by a human observer in a nearby hide.

Using robots as leaders

Robots can be used to explore how animals select leaders and in which contexts they are willing to follow. In a study on decision-making behaviour, remote-controlled fish models (and later a robotic fish) were used to demonstrate that the decision of which path to choose in a y-maze was based on a quorum [37]. If the robotic fish took the risky path (passing a predator model) and not the safe one, it was followed by a single fish but less often by groups of two, four and eight fish. To guide groups past the predator model, two (or more) robotic fish were required. Three robots generated no additional following (compared with two robots) supporting the idea that a quorum was already reached with two leaders. If the fish had to choose between two robotic fish that were different in appearance and which moved in different directions, the decision in favour of the more popular one dramatically increased as a function of group size, as predicted by the Condorcet theorem [38].

Robots for testing models of behaviour

In the case of collective behaviours of fish schools and bird flocks, there is no shortage in the literature of mechanistic models of these systems but there is a real lack of empirical data and experimental tests [39]. Interactive robots should be used here to assess critically these models and the assumptions they are based on. For example, in the debate on modelling collective behaviour, some authors proposed metric interactions (i.e. individuals respond to the movements of near neighbours within a certain distance [40]), whereas others proposed topological ones (i.e. individuals respond to a fixed number of near neighbours largely regardless of distance [20]). To discriminate between the two model predictions, a robotic fish was used that performed a sudden change in direction relative to that of the rest of the shoal. From the response of the shoal members, it became clear that a topological model was more realistic [8]. This type of research required a robot that could enter a group and physically interact with its members.

Conclusions and future perspectives

Selection of interactive technology

Interactive technology offers a new range of possibilities for experimental work in animal behaviour. Depending on the species, the research question and the budget, different options for interactive robots are available, from lab-based systems that enable the use of different robots within relatively small spaces (Box 3) to fully autonomous devices (Figure 1). The approach used in creating 'cyborg' insects (Box 2) is bound to become even more sophisticated in the near future and should hold interesting possibilities for experimentalists who require behavioural control over one or several individuals. The strength of the cyborg approach is that the animal itself is being used rather than a machine that resembles an animal. Interactions in social insects could be manipulated in this way to explore open questions in collective behaviour research [41-43]. For example, several projects used robotic honey bees to investigate the waggle dance and the onset of information cascades [7,44]. However, if fine control of a worker becomes possible through the cyborg approach, this could open new ways to investigate this complex behaviour further.

Electronic collar technology could be used to address several interesting questions and practical conservation issues. Researchers could test predictions from the literature [18] as to what proportion in a group needs to be controlled to manipulate the whole group. In animals that have social hierarchies, one could experimentally explore which individuals exert the greatest influence during movement decisions [45]. The applications of this technology in terms of farm animals and domestic animals are clear and, in some cases, already widely explored [26–28]. However, there are two key areas where smart collar technology might be also useful for wildlife management: keeping large herbivores away from valuable crops and predators away from livestock. For example, one of the first free-ranging herds of European bison in Germany is supposed to be restricted to a particular woodland area in this way (Witte, pers. commun.).

Manipulation of interaction sequences

We described several examples above in which interactive robots have been successfully used to investigate animal behaviour. Particularly in the contexts of cooperation and agonistic behaviour, the use of interactive robots could pave the way for further progress. For example, in the case of predator inspection behaviour, the place of one individual could be taken by an interactive robot that could follow different types of interaction programme depending on which aspect of cooperation or defection should be simulated (e.g. risk sharing by sharing the lead or return to the group). Box 3 shows that a methodology for this type of experiment exists [8]. By giving the robot different identities (through different body patterns or odours), it would also be possible to test whether individuals that frequently defect (while controlling for other behavioural or morphological differences) are avoided as partners for predator inspection in future. Furthermore, this approach could establish how many different cooperation partners can be remembered and for how long.

Agonistic behaviour in the form of territorial displays of individuals is another case in point. The behaviour of the rival males often strongly depends on what the opponent does [46,47] and this could be investigated systematically with an interactive robot. For the study of winner and loser effects, it might be possible to stage fights between robots that mimic conspecific males and to study what the audience (i.e. males or females that watch the behaviour) can learn from such interactions. The use of two robots for fight sequences would allow standardisation of interactions within and between fights so that one can control what each individual audience member watches at any one time.

Robots to embody personality types

Robots could be used to decouple experimentally behaviour and morphology by systematically manipulating different aspects of morphological and behavioural traits to investigate their relative importance. The latter could include personality type, which would enable an assessment of the role of personalities in decision-making processes and in social networks [48]. Social networks can be generated on the basis of interactions, spatial proximity, relatedness or other factors [49]. Social network analysis provides many new metrics to characterise the social fine structure of populations [49,50] and, therefore, an opportunity to gain an understanding of the role that different personalities have in groups and populations with regards to the transmission of information or disease or in terms of cooperation and policing of social conflicts [51,52]. How an individual can build up a certain network position and what influence this position offers could be tested experimentally through interactive robots providing novel insights into the social organisation of animals.

Different studies have described the development of behavioural differentiation in groups (e.g. in cases where food accessibility was made difficult). For example, a proportion of individuals might specialise in stealing food from others, or in joining others that have already located food [53,54]. Introducing specialised robots that mimic producer–scrounger behaviour within the group might show how the proportion of different specialists is modified. Similarly in insect societies, the introduction of robots as workers and how these modify the pattern of division of labour could be investigated.

Robots as demonstrators

The cross-disciplinary study of imitation and social learning in robots, humans and animals has emerged in recent years [55]. Animal behaviour experiments would benefit enormously from having robotic 'demonstrators' to explore the transmission process of copying behaviour. The experiments on leadership in fish decision-making discussed earlier are just the beginning of this new field [37,38]. We described experiments on fish (in the section above 'Using robots as leaders') in which the phenotypic characteristics of leaders were manipulated to explore the willingness of conspecifics to follow, but this approach could be pushed further to also investigate the willingness to copy behaviours and socially learn. Furthermore, the manipulation of the behaviour of the demonstrator could provide new important insights into what information observers can extract from watching demonstrators (e.g. when exploiting a food patch). Female robots could be a useful tool in experiments on mate-choice copying. The robot could simulate a preference for a particular male and the strength of this preference could be precisely controlled in a robot so that copying behaviour from females could be studied in detail. Robotic demonstrators could demonstrate behaviours with different error rates, which would address the question of whether it is easier to learn from individuals that make mistakes.

Young animals can be imprinted on robots interacting with them [56]. An interesting area for application is the use of robots for guiding young of the year that have been imprinted on the robot (which embodies a parent) along a suitable migration route or away from danger. Previously, geese, cranes and other species [57] have been imprinted on costumed humans (who mimic the parent species) and trained to follow a light aircraft. This approach could be expanded to other species and contexts with robots that mimic the respective species and can replace both humans and light aircraft.

Swarm intelligence and swarm robotics

In the context of collective behaviour, swarm intelligence has attracted much interest [58,59]. The role of the cognitive abilities of individuals in the decision-making process of groups is still relatively poorly understood, which opens many possibilities for experimental work. How the information that individuals provide is processed could be investigated with robots that inject preselected bits of information into the decision-making process. This is not to say that this type of work can only be carried out with interactive robots. Several studies [29,60] showed how trained or instructed individuals can be used to initiate new behaviours in groups. However, the latter does not provide the same degree of control as robots because of inter- and within-individual variation (e.g. owing to changes in motivation).

Swarm robotics [61] is a rapidly expanding field of research that offers several interesting approaches to the study of animal behaviour. Automated recognition of social behaviours can be used to assess the behavioural repertoire of an individual or a species (similar to classical ethograms) and to calculate transition probabilities between different behaviours to develop dynamic models of

the behavioural architecture of organisms [3]. Robots can then be used to embody these models. Going one step further, swarm robotics could also facilitate the study of evolutionary processes by mutating and evolving robot social behaviour, which could provide novel predictions for the study of communication and adaptive behaviour [5,62,63]. Symbrion (symbiotic evolutionary robot organisms) is a project that goes even further by aiming to model, in a self-assembling swarm of robots, generic processes within biology, such as morphogenesis, energy homeostasis and immune responses to faults [64].

Interactive robots therefore offer exciting new opportunities for experimental research. With the help of robots, complex interaction sequences can be manipulated, and behaviour and morphology can be decoupled. Robots can act as leaders and demonstrators and could even be used to embody personality types in social networks. These methodological advances facilitate novel experimental work that will push the boundaries of behavioural research.

Acknowledgements

We thank Iain Couzin, Laurent Keller, Kevin Laland, Naomi Leonard, Chris Melhuish, Tommaso Pizzari, Guy Theraulaz, Ashley Ward, Barbara Webb and four anonymous referees for their input. Funding was provided to JK by NERC (NE/D011035/1).

References

- $1\,$ Tinbergen, N. (1951) The Study of Instinct, Oxford University Press
- 2 Winfield, A.F.T. (2009) Foraging robots. In Encyclopaedia of Complexity and System Science (Meyers, R.A., ed.), pp. 3682–3700, Springer
- 3 Balch, T. et al. (2006) How multi-robot systems research will accelerate our understanding of social animal behavior. Proc. IEEE 94, 1445–1463
- 4 Halloy, J. et al. (2007) Social integration of robots into groups of cockroaches to control self-organised choices. Science 318, 1155–1158
- 5 Mitri, S. et al. (2009) The evolution of information suppression in communicating robots with conflicting interests. Proc. Natl. Acad. Sci. U.S.A. 106, 15786–15790
- 6 Michelsen et al. (1992) How honeybees perceive communication dances, studied by means of a mechanical model. Behav. Ecol. Sociobiol. 30, 143–150
- 7 Landgraf, T. et al. (2008) Design and development of a robotic bee for the analysis of honeybee dance communication. Appl. Bion. Biom. 5, 157–164
- 8 Faria, J.J. et al. (2010) A novel method for investigating the collective behaviour of fish: introducing 'Robofish'. Behav. Ecol. Sociobiol. 64, 1211–1218
- 9 Patricelli, G.L. et al. (2002) Male displays adjusted to female's response macho courtship by the satin bowerbird is tempered to avoid frightening the female. Nature 415, 279–280
- 10 Vaughan, R. et al. (2000) Experiments in automatic flock control. Robo. Auton. Syst. 31, 109–117
- 11 Ishii, H. et al. (2006) Experimental study on task teaching to real rats through interaction with a robotic rat. Lect. Not. Comp. Sci. 4095, 643–654
- 12 Walters, M.L. et al. (2008) Avoiding the uncanny valley: robot appearance, personality and consistency of behavior in an attentionseeking home scenario for a robot companion. Auton. Robot. 24, 159– 178
- 13 Dautenhahn, K. et al. (2009) KASPAR a minimally expressive humanoid robot for human-robot interaction research Special issue on 'Humanoid Robots'. Appl. Bion. Biom. 6, 369–397
- 14 Webb, B. (2000) What does robotics offer animal behaviour? Anim. Behav. 60, 545–558
- 15 Holland, O. and McFarland, D. (2001) Artificial Ethology, Oxford University Press
- $16\,$ Knight, J. (2005) Animal behaviour: when robots go wild. Nature 434, 954–955
- 17 Webb, B. (2008) Using robots to understand animal behavior. Adv. Stud. Behav. 38, 1–58

- 18 Couzin, I.D. et al. (2005) Effective leadership and decision-making in animal groups on the move. Nature 433, 513–516
- 19 Buhl, J. et al. (2006) From disorder to order in marching locusts. Science 312, 1402–1406
- 20 Ballerini, M. et al. (2008) Interaction ruling animal collective behavior depends on topological rather than metric distance: evidence from a field study. Proc. Natl. Acad. Sci. U.S.A. 105, 1232–1237
- 21 Nagy, M. et al. (2010) Hierarchical group dynamics in pigeon flocks. Nature 464, 890–893
- 22 D'Eath, R.B. (1998) Can video images imitate real stimuli in animal behaviour experiments? *Biol. Rev.* 73, 267–292
- 23 Baldauf, S.A. et al. (2008) Technical restrictions of computermanipulated visual stimuli and display units for studying animal behaviour. Ethology 114, 737–751
- 24 Moiseff, A. and Copeland, J. (2010) Firefly synchrony: a behavioral strategy to minimize visual clutter. Science 329, 181
- 25 Rosenthal, G.G. and Evans, C.S. (1998) Female preference for swords in Xiphorous helleri reflects a bias for large apparent size. Proc. Natl. Acad. Sci. U.S.A. 95, 4431–4436
- 26 Tiedemann, A. et al. (1999) Electronic (Fenceless) Control of Livestock, Technical Report PNW-RP-510, United States Department of Agriculture, Forest Service.
- 27 Butler, Z. et al. (2006) From robotics to animals: virtual fences for controlling cattle. Int. J. Robot. Res. 25, 485–508
- 28 Schwager, M. et al. (2008) Data-driven identification of group dynamics for motion prediction and control. J. Field Robot. 25, 305–324
- 29 Dyer, J.R.G. et al. (2009) Leadership, consensus decision making and collective behaviour in human crowds. Philos. Trans. R. Soc. B 364, 781–789
- 30 Conradt, L. et al. (2009) 'Leading according to need' in self-organizing groups. Am. Nat. 173, 304–312
- 31 Sato, H. et al. (2009) Remote radio control of insect flight. Front. Integr. Neurosci. 3, DOI: 10.3389/neuro.07.024.2009
- 32 Sato, H. and Maharbiz, M.M. (2010) Recent developments in the remote radio control of insect flight. Front. Neurosci. 4, DOI: 10.3389/fnins.2010.00199
- 33 Maharbiz, M.M. and Sato, H. (2010) Cyborg beetles. Sci. Am. 303, 94–99
- 34 Correll, N. (2006) SwisTrack: a tracking tool for multi-unit robotic and biological systems, In IEEE/RSJ International Conference on Intelligent Robots and Systems, pp. 2185–2191
- 35 Reaney, L.T. (2009) Female preference for male phenotypic traits in a fiddler crab: do females use absolute or comparative evaluation? *Anim. Behav.* 77, 139–143
- 36 Patricelli, G.L. et al. (2006) Male satin bowerbirds *Ptilonorhynchus violaceus*, adjust their display intensity in response to female startling: an experiment with robotic females. *Anim. Behav.* 71, 49–59
- 37 Ward, A.J.W. et al. (2008) Quorum decision-making facilitates information transfer in fish shoals. Proc. Natl. Acad. Sci. U.S.A. 105, 6948–6953
- 38 Sumpter, D.J.T. et al. (2008) Consensus decision-making by fish. Curr. Biol. 18, 1773–1777
- 39 Krause, J. and Ruxton, G.D. (2010). Living in groups: selected topics. In Social Behaviour: Genes, Ecology and Evolution (Szekeley, T., et al., eds), Cambridge University Press, pp. 203–225.

- 40 Couzin, I.D. et al. (2002) Collective memory and spatial sorting in animal groups. J. Theor. Biol. 218, 1–11
- 41 Camazine, S. et al. (2001) Self-Organization in Biological Systems, Princeton University Press
- 42 Sumpter, D.J.T. and Pratt, S.C. (2009) Quorum responses and consensus decision making. *Philos. Trans. R. Soc. B* 364, 743–753
- 43 Conradt, L. and List, C. (2009) Group decisions in humans and animals: a survey. *Philos. Trans. R. Soc. B* 364, 719–742
- 44 Kirchner, W.H. and Towne, W.F. (1994) The sensory basis of the honeybees dance language. Sci. Am. 270, 74-80
- 45 King, A.J. et al. (2008) Dominance and affiliation mediate despotism in a social primate. Curr. Biol. 18, 1833–1838
- 46 Alcock, J. (2009) Animal Behaviour: An Evolutionary Approach, Sinauer Associates
- 47 McGregor, P.K. (ed.) (2005) Animal Communication Networks, Cambridge University Press
- 48 Krause, J. et al. (2010) Personality in the context of social networks. Philos. Trans. R. Soc. B 365, 4009–4016
- 49 Croft, D.P. et al. (2008) Exploring Animal Social Networks, Princeton University Press
- 50 Krause, J. et al. (2007) Social network theory in the behavioural sciences: potential applications. Behav. Ecol. Sociobiol. 62, 15–27
- 51 Flack, J.C. et al. (2006) Policing stabilizes construction of social niches in primates. Nature 439, 426–429
- 52 McDonald, D.B. (2007) Predicting fate from early connectivity in a social network. Proc. Natl. Acad. Sci. U.S.A. 104, 10910–10914
- 53 Mottley, K. and Giraldeau, L.A. (2000) Experimental evidence that group foragers can converge on predicted producer-scrounger equilibria. Anim. Behav. 60, 341–350
- 54 Grasmuck, V. and Desor, D. (2002) Behavioural differentiation of rats confronted to a complex diving-for-food situation. *Behav. Proc.* 58, 67– 77
- 55 Nehaniv, C. and Dautenhahn, K., eds (2007) Imitation and Social Learning in Robots, Humans and Animals, Cambridge University Press
- 56 Gribovskiy, A. et al. (2010) Towards mixed societies of chickens and robots, In Proceedings of the 2010 IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS), pp. 4222–4228
- 57 Urbanek, R.P. et al. (2010) Winter release and management of reintroduced migratory Whooping Cranes Grus americana. Bird Cons. Inter. 20, 43–54
- 58 Couzin, I.D. (2009) Collective cognition in animal groups. Trends Cogn. Sci. 13, 36–43
- 59 Krause, J. et al. (2010) Swarm intelligence in animals and humans. Trends Ecol. Evol. 25, 28–34
- 60 Reebs, S.G. (2000) Can a minority of informed leaders determine the foraging movements of a fish shoal? *Anim. Behav.* 59, 403–409
- 61 Şahin, E. and Winfield, A.F.T. (2008) Special issue on swarm robotics. Swarm Intell. 2, 69–72
- 62 Floreano, D. et al. (2007) Evolutionary conditions for the emergence of communication in robots. Curr. Biol. 17, 514–519
- 63 Floreano, D. and Keller, L. (2010) Evolution of adaptive behaviour in robots by means of Darwinian selection. PLoS Biol. 8, e1000292
- 64 Levi, P. and Kernbach, S., eds (2010) Symbiotic Multi-Robot Organisms: Reliability, Adaptability, Evolution, Springer