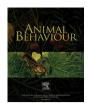
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Special Issue: Biohybrid Systems in Animal Behaviour

Active interactions between animals and technology: biohybrid approaches for animal behaviour research

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Keywords: behavioural control behavioural monitoring biomimetic robotics ethorobotics interspecies interaction sensory integration Biohybrid approaches (where living and engineered components are combined) provide new opportunities for advancing animal behaviour research and its applications. This review article and accompanying special issue explores how different types of novel technologies can be used in the field of animal behaviour from three perspectives: (1) comprehension, (2) application and (3) integration. Under the perspective of 'comprehension,' we present examples of how technologies like virtual animals or robots can be used in experimental settings to interact with living animals in a standardized manner. Such interactions can advance our understanding of fundamental topics such as mate choice, social learning and collective behaviour. Under 'application,' we investigate the potential for technologies to monitor, react and interact with animals in a variety of scenarios. For example, we discuss how drones can be used to keep large herbivores away from valuable crops and robotic predators to deter invasive species. Under 'integration,' we discuss possibilities for the coexistence of engineered and biological systems, augmenting the capacity or resilience of either or both components. Integration can be physical, for example, livestock can have sensors sit in their inner body for temperature monitoring, or within the environment, where sensors or robots monitor and interact with animals, such as a short-term earthquake forecasting method. Based upon these three themes, we discuss and classify existing biohybrid animal behaviour research, including the four articles included in our special issue. We also consider the ethics of this

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emerging field, highlight the advantages and potential issues associated with using technologies to create biohybrid systems and emphasize how such technologies can support the advancement of animal behaviour research.

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In the mid-20th century, Niko Tinbergen, a Nobel Prize laureate for his research on individual and social behaviour, conducted a famous experiment to study herring gulls, Larus argentatus, where he used wooden gull heads to study chick feeding behaviour (Tinbergen, 1948). By presenting the chicks with an artificial gull beak, he showed that the chicks would peck at the red spot on the artificial beak, just as they did at the red patch on the lower mandible of their parent's yellow beak. By using a replica of the gull beak, Tinbergen could demonstrate the specific stimuli that triggered the chicks' innate pecking behaviour. This experiment combined living biological components with artificial elements. Today, with the rapid development of engineered technologies, we are seeing a growth in biohybrid approaches, where living and engineered components are combined, for research in animal behaviour (see Table 1 for a glossary of terms). More and more researchers are developing such systems to explore and advance the field, building on the legacy of Tinbergen's foundational work. This review article introduces a Special Issue on this topic and is the result of an interdisciplinary workshop that took place at Swansea University, U.K., in autumn 2023, supported by the Association for the Study of Animal Behaviour (ASAB).

The ASAB workshop assessed and reported how biohybrid approaches are being used now and their future potential for blue skies and applied research in animal behaviour. We brought together researchers from biology, engineering and the interplay of both disciplines. Here, we report and expand on workshop discussions. We begin by providing definitions and context related to our understanding of biohybrid systems and biohybrid methods in animal behaviour, which, during our workshop, was critical to ensure engineers and biologists were able to communicate effectively on the topic discussions that followed. Next, we describe three themes that emerged during discussions, which we used to classify existing and potential research, and we introduce the collection of articles in this special issue. We end by discussing ethical considerations and outlook for this exciting and emerging research field.

WHAT IS A BIOHYBRID SYSTEM IN ANIMAL BEHAVIOUR?

We had a long discussion on how to define biohybrid systems in animal behaviour during our workshop. This was a necessary step to facilitate successful interdisciplinary collaboration. We concluded that a biohybrid system in animal behaviour is a twoway active interaction between its living and engineered components (Fig. 1a). For instance, a living fish and a virtual or robot replica of a fish responding to one another's movement is a biohybrid system (e.g. Amichay et al., 2024; Landgraf et al., 2016; Polverino et al., 2022). However, one-way interactions where the behaviour of the engineered component affects or determines the behaviour of the living component, or vice versa, are also of interest and relevance to the animal behaviour community. For instance, a study on antipredator behaviour using living fish reacting to the movement of a remote-controlled replica of a bird (Fürtbauer et al., 2015) was considered a biohybrid method in animal behaviour. It was also agreed that an active interaction was required from one component (for a biohybrid method) or both components (for a biohybrid system). As such, passive integration of biological and engineered components does not qualify under our definition, such as the automated tracking of animal motion through fixed cameras in the lab (e.g. Dell et al., 2014). Similarly, bioinspiration, for example, where the movement of underwater vehicles or robots mimic the swimming patterns of fish or snakes, focusing on biomechanical and energetic aspects of movement (Bianchi et al.,

Table 1

Term	Definition
Animal behaviour	The scientific study of the way animals interact with each other, with other organisms and with their environment
Applied research	Scientific study that focuses on solving practical problems or developing specific applications
Active interaction	The dynamic relationship between two components of a system, with the behaviour of (at least) one component being influenced by the behaviour or state of the other
Biohybrid method in animal behaviour	An approach that involves a one-way active interaction between at least one living nonhuman organism and at least one engineered component, with the behaviour of the living affecting or determining the behaviour of the engineered component, or vice versa
Biohybrid system	A system combining living biological components (from cells/tissue to organisms) with artificial engineered elements
Biohybrid system in animal behaviour	A subset of biohybrid systems that involves a two-way active interaction between at least one living nonhuman organism and at least one engineered component
Bioinspiration	An approach where an engineered system draws ideas from biological systems
Blue skies research	A scientific study that focuses on the intrinsic scientific value of the acquired knowledge without a direct link to real-world applications, also called 'basic' or 'fundamental' research
Conservation research	Scientific study concerned with the protection, preservation, management and restoration of the natural environment
Cyborg	The organism resulting from the integration of engineered components into a living organism in a way that allows the behaviour of the living organism to be altered
Ethorobotics	Research field that uses principles of the study of animal behaviour to study and develop robotic systems
Passive integration	A combination of biological and engineered components where neither component is affected by the presence or behaviour of the other, often an association
Robot	A programmable machine that can perform tasks automatically, often with sensors and mechanical actuators
Self-organization	The process through which order at a global level arises from local interactions among individuals
Swarm robotics	The employment and study of groups of robots that coordinate their behaviour to achieve tasks collectively. Swarm robotics relies on principles of self-organization and is often bioinspired
System	A set of interacting components, processes, or behaviours; can be biological or artificial
UAV	Unmanned aerial vehicle, or drone, is an aircraft that operates without a human pilot on board. UAVs can be remotely controlled by a human operator or autonomously guided by onboard computers

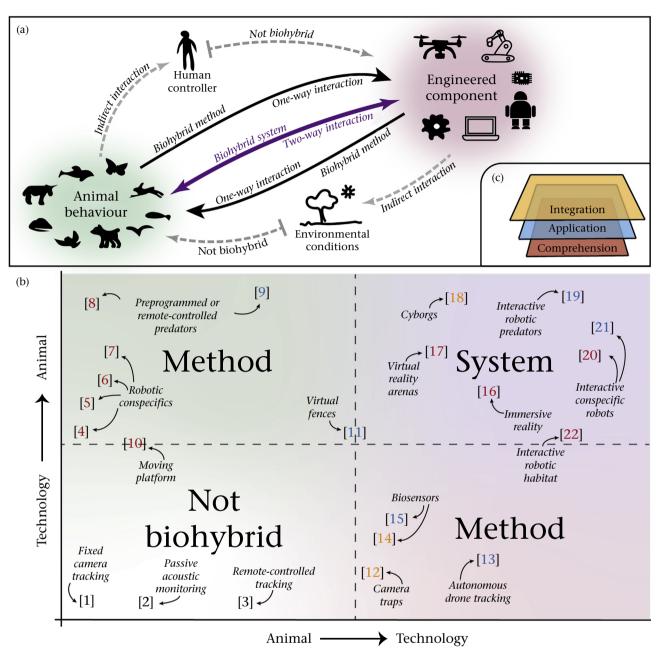


Figure 1. Classification of a method or system as biohybrid across our three Themes. (a) One-way active interactions between the behaviour of an animal and an engineered system are classified as biohybrid methods (solid black arrows), two-way active interactions are classified as biohybrid systems (solid purple arrow), and indirect interactions through human control (e.g. remote-controlled drones) or environmental conditions (e.g. temperature) are not considered biohybrid (dotted grey arrows). (b) Landscape of current research through selected representative examples. The horizontal axis indicates the intensity to which the engineered components of the system. The colour gradient of the background reflects the gradient nature of these interactions: animals being affected by technology (green), technology reacting to the behaviour of animals (red), or the active two-way interactions only and are therefore classified as biohybrid asstems, whereas examples in the other top-left and bottom-right quadrants involve one-way interactions only and are therefore classified as biohybrid methods. Examples in the bottom left quadrant (white) do not involve active interactions and are therefore not biohybrid. Example studies are given a label that captures their methodology and a colour that reflect their theme according to our classification (as in [c]). They are placed approximately on the plot. (1) Dell et al. (2014), (2) Ostreich et al. (2024), (3) Rathore et al. (2023), (4) Partan et al. (2009), (5) Clark et al. (2015), (6) Wilde et al. (2023), (7) Bierbach, Landgraf, et al. (2018), (18) Meanno et al. (2017), (16) Dolins et al. (2017), (17) Stowers et al. (2017), (18) Doan and Sato (2016), (19) Polverino et al. (2022), (20) Landgraf et al. (2016), (21) Chemtob et al. (2020) and (22) Barmak et al. (2023). (c) Representation of the layering of our three. Themes: fundamental research under Comprehension supports Applications that can be extended to the full Integration of the biological and the engineered components.

2024; Li et al., 2020) does not meet our definition. Examples in which the interaction is minimal, for instance, camera traps where motion triggers the activation of the engineer component (Mitterwallner et al., 2024; Nakagawa et al., 2023), were considered a grey area, but overall, workshop participants agreed that they met our definition of a biohybrid method.

Such clear definitions were essential for guiding interdisciplinary discussion during our workshop and therefore are expected to be similarly useful for readers from diverse fields interested in this emerging topic of research. By considering the way in which biological and engineered components interact, and whether the interaction is one-way or two-way, we were able to classify

examples as biohybrid systems, methods or neither (Fig. 1b). Humans can be part of this interaction loop, for example, where there is some human control/input of the engineered system by the researcher, but in all cases, the interaction must include one or more animals. Engineered components that indirectly affect behaviour via interaction with abiotic components (e.g. temperature or light), with or without human involvement, are not considered here to keep our focus on studies that directly affect animal behaviour. For further discussion on these and previous classifications of biohybrid research (Romano et al., 2019), see our Discussion section. Throughout the rest of the article, we will use the term biohybrid approaches to refer to both biohybrid methods and systems in animal behaviour.

BIOHYBRID APPROACHES IN ANIMAL BEHAVIOUR

Following our workshop discussions, three themes emerged: 'comprehension,' 'application' and 'integration' (Fig. 1c), which became useful for grouping existing and potential biohybrid approaches for advancing animal behaviour research. Our idea was that biohybrid research could focus on answering fundamental open questions in animal behaviour (comprehension), for a specific 'real-world' goal (application), or involving a more permanent coexistence between living and engineered components (integration). A study could fall under just one or all themes, and we noted that it is common for a research project to start with a fundamental question, later realize a potential application and, in some instances, have the potential to develop into a full integration (Fig. 1c). Below, we provide a brief introduction to biohybrid methods and systems in each theme, and in the sections that follow, more concrete examples from the literature are given.

'Comprehension' covers biohybrid methods and systems with the goal of better understanding the mechanisms, causes or consequences of animal behaviour. Work under this theme is often described as blue skies research without immediate applications or impacts outside the field of animal behaviour, and it is usually conducted within an experimental framework. For instance, studying an organism in an engineered and controllable environment (Amichay et al., 2024; Griparić et al., 2017), or while interacting with a robotic or simulated conspecific (Faria et al., 2010) or heterospecific (Fürtbauer et al., 2015; Polverino et al., 2019), enables the identification of the specific cues and signals that organisms react to and interact with, such as the biomimetic locomotion of a robot (biohybrid method, without the robot reacting to the animal; Marras & Porfiri, 2012). A classic example of biohybrid system in this category is laboratory experiments on leadership, with a robot replica of a fish and a living fish coordinating their motion (see Landgraf et al., 2016; Maxeiner et al., 2023, but also Rashid et al., 2012 for an example on an aquatic crustacean, Artemia salina). In this way, researchers can understand the specific movement cues that elicit follower behaviour. Similarly, biohybrid methods can enable innovative ways for engineered systems to record animal behaviour. Here, the interaction is one-way, for example, drones actively follow the study animals (Schad & Fischer, 2023) or on-animal tags change their sampling rate depending on the animal behaviour (Tanigaki et al., 2024), but the animals are not intended to respond to or interact with the engineered system.

'Application' involves biohybrid methods and systems that are intended to elicit changes in the behaviour of one or both, respectively, of the interacting components (living and engineered) towards a specific goal. Studies classified in this theme are often described as applied research, focusing on solving practical problems. Applications of biohybrid methods are numerous. For example, biosensors can sit inside the rumen of livestock for temperature and pH sensing, and smart collars can be used to monitor and react to the health or the position of the animal when it moves into a specific area or crosses a boundary (Lee & Campbell, 2021; Neethirajan et al., 2017). In these examples, the animal's behaviour is largely unaffected by the engineered system, but the engineered system actively collects information on the animal's behaviour for the purpose of informing interventions. Existing biohybrid systems under the application theme are taking the methods one step further: the engineered components that monitor the changes in an animal's state or surroundings can directly enact appropriate interventions or responses. This could include emitting warning signals in response to potential threats (Wikelski et al., 2020) or guiding livestock to or from specific areas (King et al., 2023). Typically, the application of biohybrid methods and systems is only possible after a baseline level of comprehension has been achieved. For example, when attempting to herd or control the movement of an animal group with a drone, you first need to understand how individuals and groups respond to the presence of drones (King et al., 2023).

'Integration' in biohybrid systems involves a complete coexistence of the engineered and the biological components, outside of experimental settings, with the goal of improving the performance of either the biological or engineered component. The nature of integration therefore means that integrated approaches are, by definition, a biohybrid system. Work under this theme is distinctive from research in the application theme in that the interaction and/ or goal is more permanent or long term (but see also van Wynsberghe & Donhauser, 2018 for a review of environmental robotics). First, a living component can enhance the capabilities of an engineered component, such as biohybrid devices that interface with an animal's nervous system to augment its ability to detect specific stimuli (Romano et al., 2019). Second, engineered components can enhance the efficiency or productivity of biological components in a system. For instance, terrestrial robots may exist permanently within a herd of cattle in an agricultural environment and interact with individuals to provide enrichment or other resources in response to specific behavioural cues or responses (Stygar et al., 2021). However, such two-way interactions in animal behaviour are still rare, and passive monitoring is more common and routinely employed (Caja et al., 1999). Note that, like passive tracking systems in the comprehension theme, leveraging principles of animal behaviour to design interactive robots (e.g. robot swarms capable of coordinated tasks, see Dorigo et al., 2021) is bioinspiration, and not a biohybrid method or system. True biohybrid systems in the integration theme are challenging for animal behaviour research, especially due to the moral and ethical considerations they raise (Dodd, 2014; Mazzolai & Laschi, 2020). It is nonetheless an important theme that the animal behaviour community should consider, what level of integration is acceptable, and for how long?

COMPREHENSION (THEME 1)

Biohybrid approaches have already enabled a unique perspective into many fundamental aspects of animal behaviour. The most common interactive technologies are autonomous or remotecontrolled robots (Krause et al., 2011) and virtual reality (VR; Stowers et al., 2017; Fig. 2). Robots and VR provide researchers with the ability to define sequences of interactions between the engineered component and the study animal(s) and directly probe and test mechanisms of behaviour (Faria et al., 2010). Work in this area is extensive, with studies related to species recognition (e.g. Macedonia et al., 2013), social learning (Chimento et al., 2021; Romano et al., 2021, 2022), predator–prey identification (e.g. Ord et al., 2021), alarm calls (Partan et al., 2009) and interspecific interactions (Bierbach, Lukas, et al., 2018; Worm et al., 2021). For

instance, a robotic bee (Fig. 2a) has been used to decode the 'dance language' of honey bees, *Apis mellifera*, where robots mimicking the dance signals of the bees (Landgraf et al., 2008; Michelsen et al., 1992) allow for a deeper understanding of the link between social information and behaviour (Landgraf et al., 2021). The level of biomimetism of robotic individuals varies, ranging from using taxidermy (Fig. 2b; Partan et al., 2009; Patricelli & Krakauer, 2010) or a 3D printed model of an organism (Fig. 2c and d) containing the engineered components (Wilde et al., 2023) to more abstracted representations of animal morphology (Fig. 2e–h; Landgraf et al., 2016, 2010; Storms et al., 2022), with or without biomimetic locomotion (Marras & Porfiri, 2012; Polverino et al., 2019; Storms et al., 2022). More examples of robotic replicas in animal behaviour research are given in Fig. 2, and below, we further elaborate on key areas of successful use cases of robots (Fig. 2i) and VR (Fig. 2j–l) in the context of mate choice, predator—prey dynamics, sensory ecology and collective behaviour.

In the case of mate choice, artificial individuals can help us determine which morphological or behavioural characteristics are particularly important in driving sexual selection. Robotic replicas of male bluefin killifish, *Lucania goodei*, where the replica fish's body size, coloration and motion pattern could be controlled, enabled systematic study of female preference in the lab (Phamduy et al., 2014; Fig. 2h). In the field, a 3D-printed fiddler crab, *Afruca*

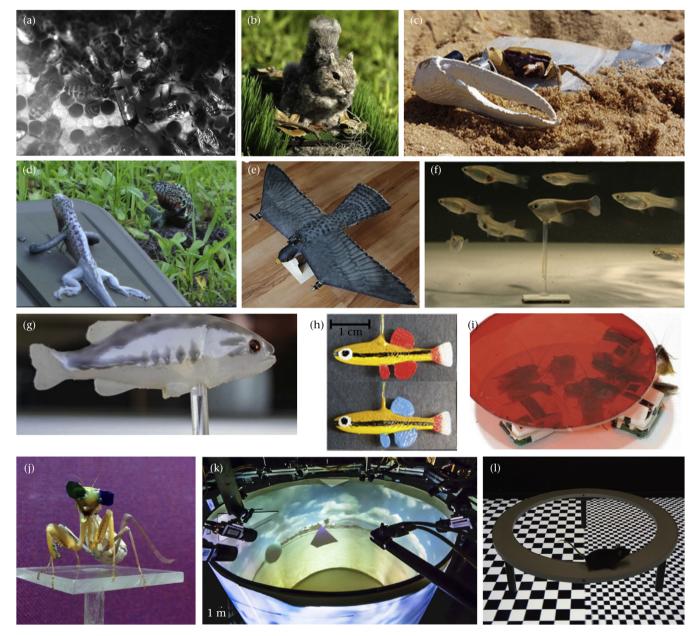


Figure 2. Examples of biohybrid methods and systems in animal behaviour. (a) Biomimetic bee on the comb surface, modified from Landgraf et al. (2010). (b) Squirrel robot producing alarm calls, modified from Partan et al. (2009). Photo: Jason Marsh. (c) Biomimetic robot fiddler crab, modified from Wilde et al. (2023). (d) Robot lava lizard interacting with a male individual. Snapshot taken from a video by Clark et al. (2015). (e) Biomimetic robotic falcon with stable wings, taken from Storms et al. (2022). Photo: Robert Musters. (f) A guppy-like replica of the RoboFish system, moving in a tank with real guppies, modified from Bierbach, Landgraf, et al. (2018). Photo: David Bierbach. (g) Bioinspired replica of a fish predator (Polverino et al., 2019, 2022). Photo: Giovanni Polverino. (h) Replicas of an adult male killifish with different colorations, modified from Phamduy et al. (2014). (i) Robots aggregating with real cockroaches under an artificial shelter, modified from Halloy et al. (2007). (j) Mantis wearing coloured 3D glasses in the experimental platform, modified from Nityananda et al. (2016). (k, l) Examples from the VR system FreemoVR, the flight arena 'Flycave' with three projectors (k), and the walking arena 'MouseVR' with a television display (l), modified from Stowers et al. (2017). Further details about the artificial individuals shown here are given in Table 2.

tangeri, programmed to wave using its large major claw was used to study male-male interactions and signals of competition and male quality (Wilde et al., 2023; Fig. 2c). At a larger scale, biohybrid methods can enable the study of whole mating populations in the wild. For instance, 'lekking' is a mating behaviour where males gather in a specific area, known as a lek, to display and compete for the attention of visiting females (Patricelli & Krakauer, 2010). Understanding lekking behaviour is fundamental for sexual selection research, but collecting data on these mating interactions in the wild is challenging. Rathore et al. (2023) overcame challenges in studying lekking in the wild by using drones to track individual blackbucks, Antilope cervicapra, instead of traditional field observation techniques, such as focal sampling (Nefdt, 1995). This approach (passive, images) could be extended to work as a biohybrid method, where drones could self-organize to cover the full lek (~40 000 m² area) and monitor mate choice autonomously, enabling the quantification of spatiotemporal dynamics within the lek and decreasing the funds and manpower needed to implement methodologies with several human-controlled drones.

Another field revolutionized by the development of more biohybrid approaches is the study of sensory ecology. Using VR (Engert, 2013; Naik et al., 2020), researchers can control an individual's sensory input and quantify its behavioural reaction or even neurological responses to external stimuli. Examples include studies of height aversion in mice (Fig. 21), schooling tendencies of zebrafish, Danio rerio (Stowers et al., 2017), the predation cost of leadership in virtual prey (Joannou et al., 2019) or depth perception in praying mantis, Mantis religiosa (Nityananda et al., 2016; Fig. 2j). By placing living organisms within engineered testing arenas or interacting with robotic individuals, aspects of information transfer (Barmak et al., 2023; Griparić et al., 2017) and individual or social learning (Chimento et al., 2021) have also been investigated, such as light associations to stress and food sources (Romano et al., 2022) or risk-benefit evaluations for decision making (Romano et al., 2021). When applied to animal collectives, this approach allows one to distinguish between sources of social information and decouple stimuli that are otherwise highly correlated in the real world. For instance, researchers were able to highlight the role of visual information (rather than lateral line) for coordination and schooling by studying fish swimming in physical separation but virtually together (Harpaz et al., 2021). Using VR or robots in this way enables the precise investigation of the effect of a phenotype or individual behaviour on social interactions and group decisionmaking (Lemasson et al., 2018; Sridhar et al., 2021), as demonstrated in studies manipulating robot appearance (Papaspyros et al., 2024; Polverino et al., 2012), swimming pattern (Polverino et al., 2013) and pattern of interaction with conspecifics (Bierbach, Landgraf, et al., 2018; Maxeiner et al., 2023; Wang et al., 2017). Such tools also have potential for future studies, for instance, to disentangle morphology and movement cues for social distancing and pathogen avoidance (Romano & Stefanini, 2021).

In studies of fish especially, biohybrid research has enabled the control of both predators and prey. By using responsive robotic prey in the lab, researchers found that predatory fish adapt to the predictability of the prey-escape tactics (Szopa-Comley & Ioannou, 2022). By allowing predatory fish to attack simulated virtual prey, researchers showed that virtual prey with Lévy motion were twice as likely to be targeted by the predator than virtual prey with Brownian motion (Ioannou et al., 2023). Such insight would not be possible without the use of the engineered components in these systems since traditional methods have struggled to capture the complexity of predator–prey interactions due to their dynamic nature. In this special issue, Johnston-Barrett et al. (2025) show how saltatory movement in virtual prey does not affect predation risk from stickleback fish, *Gasterosteus aculeatus*, and Szopa-Comley and Ioannou (2025) demonstrated that blue acaras consistently use pure pursuit rather than parallel navigation when targeting robotic prey, regardless of prey predictability. Sankey (2025) further showcases how such biohybrid experiments can enable the study of the evolution of collective behaviour when coupled with mutlilevel selection theory. Indeed, discussions on predator-prey dynamics featured heavily in our workshop, and we expect huge advances in studying predator-prey dynamics also in the wild. For instance, several technologies are currently combined to study multipredator and predator-prey interactions of California sea lions, Zalophus californianus, striped marlin, Kajikia audax and Pacific sardines, Sardinops sagax caeruleus (Hansen, Domenici, et al., 2023; Hansen et al., 2022; Hansen, Kurvers, et al., 2023). Like the lekking example above, these technological innovations are not biohybrid by themselves, they are passive observations using novel technologies (Fig. 1b) but provide a platform for new research possibilities using biohybrid methods. In the following subsection, we provide a detailed example of biohybrid research in animal behaviour in a challenging real-world context: the open ocean.

Case Study: Biohybrid Research in Animal Behaviour in the Open Ocean-Current Status and Future Prospects

One of the fundamental challenges of studying animal behaviour in the open ocean is the sheer scale of the environment and the ephemeral nature of observable behaviour. Particularly when applied to multispecies interactions such as predator aggregations (Hansen, Kurvers, et al., 2023), being in the right place at the right time to not only observe but also quantify interactions between and within species has proven a logistical problem for decades. Thus, despite marine animal behaviour being a long-established field, advancements in technology and robotics are the key to capturing these events and opening up new avenues of research, allowing us unprecedented insight into marine ecosystems, species behaviour and oceanographic processes (Burns et al., 2024; King et al., 2018). One such example is the group hunting of striped marlin, Kajikia audax, on schools of Pacific sardines, Sardinops sagax (Hansen et al., 2022), whose characteristics and dynamics would be impossible to systematically study with just traditional tools from behavioural ecology; we describe the methodological set up that enabled its study below.

Using a combination of underwater and aerial video techniques, computer vision, boat-based sonar and bioinspired robots, quantitative data of striped marlin attacking schools of baitfish could be collected over many consecutive seasons. A methodological package that includes both traditional ethological techniques combined with biohybrid systems, and advancing technology has solved a longstanding experimental and analytical problem, recording hunting behaviour along with the spatiotemporal data of grouping marine predators and their prey underwater and above, providing unprecedented insights into the functions and mechanisms of group-hunting behaviour in the open ocean (Burns et al., 2024; Hansen et al., 2022). Specifically, as in terrestrial ecosystems, drones can be used to obtain high-resolution spatial and temporal positioning of individuals close to the water surface for entire hunt sequences over several hours (using a drone-relay approach). In the absence of geographical landmarks, the drone movements can be localized in 3D space by integrating the inbuilt GPS coordinates, the onboard computer or inertia measurement unit and the altitude data. From the footage, combined with modelling and image-based machine learning algorithms (DeepLabv3 and Detectron2), the tracking coordinates of the objects of interest (any predators and prey present) can be obtained (Koger et al., 2023). Simultaneously, a stereo camera setup and/or underwater drone can be used for filming underwater, and similar computational tracking tools can

allow species identification, quantification of individual predator and prey positions in 3D space (Jackson et al., 2016), as well as capture rates and kinematics (speed, turning angles, radii and accelerations; Pacher et al., 2024). To visualize predators and prey at depth, digital sonar-based animal tracking (Adaptive Resolution Imaging Sonar, ARIS, Sound Metrics) and echosounders can be used. However, understanding what goes on below the surface is still a huge logistical problem to overcome, here lies perhaps the biggest opportunity for biohybrid systems.

Overall, current technologies used in the open ocean include unmanned aerial vehicles (UAVs) (equipped with cameras and other sensors), autonomous and remotely operated underwater vehicles (AUVs and ROVs), acoustic equipment (sonars, hydrophones and echosounders) and environmental sensors (e.g. Argos floats, animal-triggered cameras). All these techniques produce an overabundance of footage of animal behaviour coupled with environmental factors that are impossible to analyse manually, the development of deep learning models is necessary to process and extract behavioural data from these recordings (Nakagawa et al., 2023). Existing biohybrid tools can be further adjusted to accommodate marine research and conservation: biosensors or smart tags can be applied for behavioural modification of large species (e.g. to keep migrating whales away from shipping lanes or shark nets) or Robofish technology can be upscaled to observe predatory-prey interactions in the wild and deter or patrol species from certain areas.

APPLICATION (THEME 2)

Knowledge acquired from research under the comprehension theme (above) can further be used to alter animal behaviour and achieve a specific applied goal or undertake conservation research in the wild. Since VR and environment altering techniques are (at present) restricted to laboratory set-ups, the engineered tools used in this theme include mostly UAVs or (drones), biomimetic robots and remote sensors. To establish a big-picture view of the biohybrid approaches under this theme, we further discuss applications related to bioherding (King et al., 2023) and ecology of fear (Polverino et al., 2022; but see also Chellapurath et al., 2023; Schmickl & Romano, 2024 for conservation-focused reviews). The examples we use focus on influencing animal behaviour via the visual sensory modality, in part reflecting our own human sensory biases. However, acoustic playback (e.g. Partan et al., 2009; comprehension theme) integrated into mobile sensors (e.g. Oestreich et al., 2024) can also provide further means to alter animal behaviour in future applications.

Changing or directing the movement of animal groups in the wild (herding) has the potential to mitigate numerous negative human-wildlife interactions, for instance, redirecting elephants that pass-through villages or birds crossing airways in airports (King et al., 2023). An example of an existing application is the RobotFalcon, a radio-controlled animatronic that resembles a Peregrine falcon, Falco peregrinus, and was developed to drive away flocks from airports (Storms et al., 2022). The robotic predator elicits collective escape reactions from bird flocks of several species (Storms et al., 2024) similar to those from a real predator, something not achieved when flocks are attacked with a nonbiomimetic drone (Storms et al., 2022). Simple drones can however still elicit avoidance behaviour in animals due to their presence, as shown in southern white rhinos, Ceratotherium simum, and keep individuals within a given area as an antipoaching tactic (Penny et al., 2019). Similarly, virtual fencing (a boundary imposed without any physical barrier) or smart fences (fences with automated identification of animals and alarm systems) can be used to repel livestock and wildlife from exiting or entering a given area, but there are welfare considerations regarding the type of stimulus/cue delivered to the animals (Lee & Campbell, 2021). Self-organized groups of (autonomous) robots also have potential to be used to protect and herd livestock away from danger (Van Havermaet et al., 2023). To achieve the level of autonomy that such biohybrid system will require, computational models are needed to simulate different scenarios of interaction between robot groups and animals and identify the best strategy to achieve the desired outcome (Bartashevich et al., 2024; Papadopoulou et al., 2022; Strömbom et al., 2014).

Scaling up from altering the behaviour of individuals to influencing entire populations, biohybrid methods and systems offer a promising approach to mitigate the negative effects of pests and invasive animal species (Polverino & Porfiri, 2021). Robots inspired by natural predators can effectively repel pests and invasive species that threaten agriculture and native biodiversity. For example, a robotic predator modelled after the Guinea fowl, Numida meleagris, was used to successfully study the escape behaviour of locusts, Locusta migratoria (biohybrid method), not only providing valuable insights into predator-prey interactions (Romano et al., 2017) but also suggesting potential applications for population control (Polverino & Porfiri, 2021). Under this perspective, Polverino et al. (2019) developed a robotic predator that combines morphological and locomotion characteristics of native predators (i.e. the largemouth bass, Micropterus salmoides; Fig. 2g) to reveal the evolutionary vulnerabilities of the invasive mosquitofish, Gambusia affinis, in laboratory experiments. Nonlethal costs of predation threat by the robot increased stress responses in mosquitofish and mitigated their negative impact on native amphibians threatened by mosquitofish in the wild (Polverino et al., 2022). Interestingly, the effects of the robot carried over to the routine activity and feeding rate of mosquitofish weeks after exposure, resulting in weight loss, variations in the entire body shape and reduced fertility in both sexes, impairing the survival, reproduction and ecological success of the invaders (Polverino et al., 2022). Simultaneously, the specifics of the robotic predator did not have negative repercussions on the behaviour of native tadpoles, which, instead, benefitted from the increased stress in mosquitofish associated with the presence of the robot (Polverino et al., 2022). Overall, these techniques offer conceptual and technical advances that fill critical gaps in experimental biology and ethorobotics (Abdai & Miklosi, 2024), open the door to new opportunities for targeted experimental analyses at a larger scale and provide the scientific foundations for informing and refining biocontrol practices.

INTEGRATION (THEME 3)

The theme that generated the greatest disagreement among the workshop attendees was the longer-term integration of biological and engineered components, with some being completely opposed to coexistence or physical integration of technologies with animals, whereas others were excited by the potential for cyborgs and biohybrid societies. Regardless of the level of enthusiasm for research under this theme, it was agreed that integrative solutions can advance animal behaviour research. Our discussions focused specifically on if and how animals can coexist in the real world with robotic individuals to support biodiversity monitoring and conservation (Chellapurath et al., 2023; Schmickl & Romano, 2024) or whether smart sensors can improve the performance of either the biological or engineered component. An area in which integration appears straightforward includes biohybrid methods in farm settings, for instance, sensors can allow the constant monitoring of cattle, Bos taurus, feeding, movement, social behaviours (Occhiuto et al., 2023) and the early detection of disease (Bushby et al., 2024). Similarly, the use of animal tagging (i.e. animals carrying

biologgers: Fehlmann & King, 2016; Oestreich et al., 2024) around the world can provide data about changing ecosystems, with animals acting as environmental sentinels (Ellis-Soto et al., 2023). This concept is becoming a reality, with an international team of scientists developing this type of early warning system, named 'ICA-RUS,' an acronym that stands for International Cooperation for Animal Research Using Space animal-borne sensors. This biohybrid approach can deliver fine-scale (in space and time) data for ecological and climatic forecasting (Ellis-Soto et al., 2023). Less straightforward, from an ethical perspective, are approaches where the engineering component interacts with the animal in a more invasive manner, for example, cyborgs.

Cyborgs can be used to study fundamental questions (theme 1) or harness their sensory capabilities and control their movements (theme 2) but typically entail a semipermanent or fully permanent integration of engineered components in living organisms. Hence, our discussion of cyborgs was primarily related to our integration theme. Cyborg insects in particular, where small circuits allow the control of an insect's behaviour (Doan & Sato, 2016) or collection of its sensory data (Gupta et al., 2024), have been an expanding research field for decades, starting from biological research with backpack technologies that aimed to study their muscle and neural coordination during flight (Kutsch et al., 1993; Vo-Doan et al., 2022). Electrical neural stimulation has facilitated walking control, including turning and forward motions in American cockroaches, Periplaneta Americana (Holzer & Shimoyama, 1997), Madagascar hissing cockroaches, Gromphadorhina portentosa (Latif et al., 2016; Tran-Ngoc et al., 2023), Haitian cockroaches, Blaberus discoidalis (Sanchez et al., 2015), sideways and backward motions in darkling beetles, Zophobas morio (Nguyen et al., 2019; Vo Doan et al., 2018) and flight steering in hawk moths, Manduca Sexta (Tsang et al., 2010). Neuromuscular stimulation has enabled flight control and walking control in giant flower beetles, Mecynorrhina torquate (Cao et al., 2016; Sato et al., 2009) and jumping control in locusts, Locusta Migratoria (Ma et al., 2022). Overall, cyborg technology helps us better understand the encoding of space in animal brains (Eliav et al., 2021) and the biomechanics and neural control of flight (Agarwal et al., 2023; Sato et al., 2015; Vo-Doan et al., 2022).

Recent demonstrations of autonomous navigation and human detection using cyborg insects have shown promising potential for urban search and rescue operations (Nguyen et al., 2023; Tran-Ngoc et al., 2023) with applications ranging from defence to agricultural (Siljak et al., 2022), especially via advancements in odour identification (Gupta et al., 2024). Such cyborg technology has also been extended to birds (Jang et al., 2021) and mammals, with cyborg rats moving through a maze by human mind control (Zhang et al., 2019) and systems for collaborative rat-UAV navigation to counteract perception uncertainties and improve cyborg control (Zheng et al., 2024). This technology has also been applied to jellyfish, enabling simple propulsion control underwater, with potential future applications in monitoring ocean health (Xu & Dabiri, 2020). Despite its potential, cyborg technology raises ethical and sociological concerns (Dodd, 2014), reviewed by Siljak et al. (2022).

A less invasive type of integration is common at the ecosystem level; robots or sensors can be embedded in agricultural or wild systems to improve health or functioning, creating a longer-term integration moving beyond the Application theme (Cliff et al., 2018; Mitterwallner et al., 2024). In the future, robots could autonomously 'live' in the field to routinely inspect areas for biodiversity monitoring (Brickson et al., 2023; Mitterwallner et al., 2024, see also Pedrazzi et al., 2025 in this Special Issue) or evaluate green infrastructure, such as wildlife crossings (Soanes et al., 2024, see also Carrillo-Zapata et al., 2020 for practical information on the use of robot swarms in the workplace for bridge inspections). Engineered components can also enable interspecific information transfer, allowing different species to interact across large scales and autonomously make decisions, towards improved artificial collective intelligence and truly biohybrid 'rewired' ecosystems (Bonnet et al., 2019). Such communication networks can allow the exploitation of the sensory or locomotion abilities of living organisms to support their adaptation to environmental changes and the more organic influence of their choices by researchers or robotic systems. Given the continuous interaction between engineered components and animals in such integrative solutions, it is important to note that habituation may be a positive or negative aspect depending on the system in question: animals may stop being bothered by sensors present in their environment (positive) or by a drone that aims to guide them (negative). Given that a large part of the engineering community is excited by the possibility of embedding engineered systems into our societies (e.g. the internet of living things; Sørensen & Lansing, 2023), the animal behaviour community can play an active role in discussions and future practices on this integration.

Finally, a big step towards the creation of biohybrid systems in industry or nature is the automation of the engineered components (Carrillo-Zapata et al., 2020). The field of swarm robotics, the bioinspired coordination and control of groups of robots (Dorigo et al., 2021) can lead this effort, by producing robots that purposely interact with each other and with the ecosystem to support effective integration. A field in which such biohybrid approaches can be important in aquaculture, where monitoring and modelling of ecological parameters can improve the overall production quality and fish welfare. A conventional aquaculture net pen is large (40 000 m^3), with a depth varying between 15 m and 50 m. Being able to measure water quality parameters (e.g. dissolved oxygen, salinity and temperature) at multiple locations inside the net pen can increase fish farmers' insight into the conditions the fish experience. Indeed, sudden changes in measured parameters may indicate the presence of, for example, harmful algae or other harmful species, and it may alert the farmers that an action should be taken. Biomimetic robots can merge with fish in the net pen to provide information about the water quality conditions, monitoring chemical concentrations with increased temporal and spatial resolution. Besides, robots can actively pursue other information concerning fish movements and well-being in the cage, increasing our understanding of how fish movements change in relation to water quality. Finally, robots can interact with fish steering them towards areas of the cage where the water quality is higher, actively contributing to fish welfare. For similar large-scale and long-term biohybrid integrations in the wild, some features of the robots used should be considered: (1) the ability to blend in the environment to minimize disturbance to (and damage from) humans and nontarget species, (2) the controllability of their behaviour (and potentially their autonomy and learning ability), (3) the ease of mass fabrication and (4)the biodegradability of materials, especially for systems that aim to be fully integrated and that may malfunction, disconnect and 'die' in nature (Mazzolai & Laschi, 2020).

ETHICS

The examples we have used throughout this review have clear research outcomes. In the Comprehension theme, the intended outcome is often the furthering of scientific knowledge. In the Application and Integration themes, outcomes typically relate to solving a problem or improving the functioning of a system. In all cases, the advancement made, whether it is *blue skies* or *applied research*, must be carefully weighed against the potential for adverse consequences for the individuals, groups, populations and the wider ecosystem. For example, journals such as *Animal*

Behaviour that maintain the highest ethical standards may publish research on cyborgs, but only on instances where there are very clear, real and important benefits to animals, human society, our economy or the environment, which could not be achieved otherwise.

Many biohybrid methods and systems require trapping and/or manipulation of animals, and even where there is no direct handling of animals, these approaches can cause disruption to the animals' population or the wider ecosystem. Again, any disruption or adverse consequence needs consideration before the research can begin. One area which will undoubtedly have massive growth in animal behaviour research soon is drone research. In this special issue, Pedrazzi et al. (2025) reviewed the potential for drones to advance animal behaviour research and provide an overview of the ethical issues to consider, including the sometimes-unintentional consequences for data and privacy. Especially for cases under the integration theme, the biohybrid system needs to have protection mechanisms that guard against hacking or disruption (malicious or through malfunctions) of its engineered components (Strobel et al., 2023). More generally, we think that it is important to emphasize the potential for positive welfare outcomes from biohybrid research. Here, we briefly consider the use of animals guided by the principle of the three Rs: Replacement, Reduction and Refinement (but see also Mancini & Nannoni, 2022).

Replacement refers to methods that avoid or replace the use of animals in research. In the context of biohybrid systems, opportunities are vast for replacement under the Comprehension theme. Using robots or VR allows researchers to mimic animal behaviours and replace the need to use live animals to act as conspecific or heterospecific. Robotic individuals can replace experimental animals to decrease their number or overcome ethical considerations, especially important when studying predator-prey interactions in the lab, where the use of real predators and prey in enclosed environments should be avoided (Fürtbauer et al., 2015; Polverino et al., 2019, 2022). VR settings can help in research training related to animal handling (Tang et al., 2021) or enhance the environment and daily tasks of animals in captivity, especially nonhuman primates (Dolins et al., 2017). The use of VR can also limit or promote sensory cues, allowing researchers to disentangle their importance for the focal species, such as the work on fish lateral lines, where VR removes this cue and is much less invasive than alternative approaches that require manipulation of, or damage to, the lateral system (Faucher et al., 2010).

Reduction involves strategies to minimize the number of animals used in research. By being able to manipulate only traits of interest while controlling all other traits, standardization of stimuli is one of the major strengths of biohybrid methods and systems. This is particularly useful in field-based studies as heterogeneity in field sites and interindividual variation of both predator and prey is often unmeasured (Balaban-Feld et al., 2018; Szopa-Comley et al., 2020; VäL li et al., 2020). By standardizing the traits of at least one component in the system (e.g. by using biomimetic prey), the biohybrid approach helps reduce the unexplained variation in data sets, providing greater test power and/or reducing the need for as many replicates (with benefits for reducing the number of animals used in research, as well as the time and financial costs necessitated by research). The benefits of the biohybrid approach in the study of predator-prey interactions go even further, however, by broadening the range of questions and study systems to include employing an experimental evolution approach. This approach is exemplified by the studies of Bond and Kamil (1998, 2002), who allowed the phenotypes of virtual moths on a computer screen to vary in abundance over many generations depending on the susceptibility of the prey's appearance to real predators (blue jays, *Cyanocitta cristata*).

Refinement refers to modifying procedures to minimize pain, suffering and distress and enhance animal welfare. Under the Application theme, using biohybrid methods can allow humans to alter animal behaviour to mitigate human-animal conflict, with potential to reduce the need for poisoning, culling or other forms of population control. Using biohybrid technologies to influence pest behaviour can lead to more humane and targeted management strategies, including pest control (Polverino et al., 2022), ultimately reducing the reliance on widespread and often inhumane practices. This not only decreases the number of animals subjected to these less humane methods but also aligns research practices with higher ethical standards. Under the Integration theme, the use of animalattached sensors or sensors in the environment can provide realtime monitoring of animal health and behaviour, again, allowing early identification of health and improving welfare issues in farms (Bushby et al., 2024) and fisheries (Liang et al., 2022).

DISCUSSION

Biohybrid methods and systems provide exciting and unique tools to better understand, protect and coexist with animals. They offer great advantages over traditional approaches. First, they enable an ever-increasing detail of observation and data collection, which leads to more precise hypotheses and predictions about how nature works. Second, biohybrid approaches can expand our sensory system to that of the animals, for instance investigating the role of electric signals on social interactions (Pedraja & Sawtell, 2024) and helping us decouple social interactions (Krause et al., 2011). Moving beyond vision and high-level acoustics, technology can help us disentangle complex chemical information used in animal communication. Third, they strengthen the link between animal behaviour, neuroscience and conservation, supporting direct connections between fundamental and applied research.

This review does not aim to present a systematic search of the existing literature, and most of the studies we have presented are examples from the authors' work and areas on central themes of animal behaviour that we discussed during the workshop. For more formal consideration of the literature, we recommend also consulting previous reviews on this topic (Romano et al., 2019; van Wynsberghe & Donhauser, 2018). For instance, Romano et al. (2019) presented a systematic review of literature that includes biohybrid-related keywords from Scopus and Web of Science databases and focused on common themes across studies. Their classification identified two axes of research: physiological interactions between an animal and an artificial device, and mixed societies of animals and robots, that is, behavioural interactions between the biological (animal population) and engineered components. Within these, the authors describe the different types of existing biohybrid organisms, from controlling robots by biological input to harvesting energy from enzyme-based biofuel cells placed into living animals. In contrast, we focused here on the concepts and questions to be addressed in animal behaviour research, and we provide an overview and framework from which the subfield of biohybrid systems in animal behaviour can advance.

Apart from the approximately 30 species we have mentioned throughout our examples, many more have been involved to date across biohybrid research (Romano et al., 2019), such as studies on territorial defence in frogs (*Epipedobates femoralis*; Narins et al., 2005), laterization in ticks, *Ixodes ricinus* (Benelli et al., 2018), courtship in satin bowerbirds, *Ptilonorhynchus violaceus* (Patricelli et al., 2006) and sociality in dogs (Kubinyi et al., 2004). To keep the focus on studies relating closely to animal behaviour, we have also not discussed extensive literature on environmental management or biohybrid systems with engineered outlook, for example, harnessing energy from implanted biofuel cells (as in cyborg

10

M. Papadopoulou et al. / Animal Behaviour xxx (xxxx) xxx

Table 2

Exam	oles of existing	biomimetic	artificial	individuals	used in	h biohybrid	animal	behaviour re	esearch

Robotic species	Biohybridism	Study theme	Theme	Source
Anoles, Anolis sagrei, Anolis graham, Anolis oculatus, Anolis cristatellus	Method: Preprogrammed robot	Species recognition	С	Dufour et al. (2020);, Macedonia et al. (2013), Partan et al. (2011)
Australian brush-Turkey, Alectura lathami	Method: Preprogrammed robot	Species recognition	С	Göth and Evans (2004)
Bluefin killifish, Lucania goodei	Method: Preprogrammed robot	Coloration & mate choice	С	Phamduy et al. (2014; Fig. 2h)
Cockroach, Periplaneta americana	System: Interactive robot	Collective decision-making	C-A-I	Halloy et al. (2007; Fig. 2i)
European honey bees, Apis mellifera carnica	Method: Preprogrammed robot	Social influence	С	Landgraf et al. (2010; Fig. 2a)
Fiddler crabs, Afruca tangeri	Method: Preprogrammed robot	Sexual displays & mate choice	С	Wilde et al. (2023; Fig. 2c)
Greater sage grouse, Centrocercus urophasianus	Method: Remote-controlled robot	Sexual displays & mate choice	С	Patricelli and Krakauer (2010)
Heron, Ardeidae	Method: Preprogrammed robot	Personality and plasticity	С	Fürtbauer et al. (2015)
House finches, Carpodacus mexicanus	Method: Preprogrammed robot	Social information & foraging	С	Fernández-Juricic et al. (2006)
Largemouth bass, Micropterus salmoides	System: Interactive robot	Predator-prey interactions	C-A	Polverino et al. (2019, 2022; Fig. 2g)
Lava lizards, Microlophus grayii, M. indefatigabilis, M. occipitalis	Method: Preprogrammed robot	Species recognition	С	Clark et al. (2015; Fig. 2d)
Peregrine falcon, Falco peregrinus	Method: Remote-controlled robot	Collective escape	C-A	Storms et al. (2022; Fig. 2e)
Rat, <i>Rattus rattus</i>	System: Interactive robot	Symbiosis requirements	Ι	Ishii et al. (2004)
Squirrel, Sciuridae, Sciurini	Method: Pre programmed robot	Alarm behaviour: Social information	С	Partan et al. (2009; Fig. 2b)
Three-spined sticklebacks, Gasterosteus aculeatus	System: Interactive robot	Leadership and social influence	С	Faria et al. (2010)
Trinidadian guppies, Poecilia reticulata	System/method: Preprogrammed or interactive robot	Antipredator coloration, collective motion, social influence	С	Heathcote et al. (2020), Landgraf et al. (2016; Fig. 2f)
Zebrafish, Danio rerio	System: Interactive robot	Collective decision-making	С	Chemtob et al. (2020)

lobsters; MacVittie et al., 2012) and animal movement (Aktakka et al., 2011). Behavioural responses through environmental conditions have also been categorized as not biohybrid in our classification. Of course, abiotic factors can play a crucial role in animal behaviour, and the effect of the animals' behaviour in the wild can in turn affect its environment. However, during our workshop, we realized that we had to constrain ourselves to active interactions that are more central in the field of animal behaviour to dive deeper into each case study and highlight the advantages and potential of biohybrid approaches. We refer to van Wynsberghe and Donhauser (2018) and Chellapurath et al. (2023) for reviews on robotics and other autonomous technologies for environmental research and conservation.

The framework we presented here (Fig. 1) classifies the different types of biohybrid approaches currently used in animal behaviour research in relation to their aim and degree of interaction between biological and artificial components. It is clear that different areas of the map (Fig. 1b) are dominated by specific themes, and others are ripe for future development. For instance, there are numerous examples in the comprehension theme in the top-left quadrant (in red colour, Fig. 1b), largely because of the increasingly more common use of biomimetic artificial individuals in animal behaviour research. Although most studies tackle fundamental questions, there are also examples that extend to application and integration, but there is definitely potential to develop the existing systems within blue skies research to real-world applications (see Table 2 for existing biomimetic individuals). In contrast to the top quadrants, with most studies taking place in the lab, the bottom-right quadrant is populated by examples from the field in the application and integration themes (in blue and orange colours, Fig. 1b). This area is less populated, since technological barriers pose challenges for this type of research; sophisticated and autonomous engineered systems that can react and interact with animals are required (see our Outlook section).

Through classifying the approaches used in animal behaviour research as a biohybrid method, system or neither (Fig. 1b), it also became clear that many approaches do not meet our criteria for biohybrid, such as passive acoustic monitoring or remotecontrolled drones. However, these are vital first stages for developing a biohybrid method or system to identify important system components that should be considered (biological insight for engineers) or propose necessary technological improvements (engineered tools for biologists). Thus, to reach the integration of technologies in nature, collaborations and increased knowledge exchange between the two fields are necessary.

Despite its advantages, it is important to consider the costs and benefits while developing a new biohybrid method or system, since they may not always be the best choice for animal behaviour research. In particular, an important distinction was made among the engineers at our workshop: is the technology available 'off-theshelf' or does the technology need to be developed? The former is obviously more accessible and scalable, but self-built solutions are increasingly more accessible through open access protocols (Nakagawa et al., 2023). For example, initiatives for technology sharing (e.g. technology for wildlife foundation, www. techforwildlife.com) that guide and support animal behaviour researchers, and open-source software and hardware, like the Biohybrid Observation and Interaction (BOBI) platform, which supports the integration of wheeled robots and small mammals as a biohybird system (Papaspyros et al. 2023) are becoming more common. In addition, artificial individuals that have already been proven successful in actively interacting with animals can be reused (for a collection see Table 2).

OUTLOOK

At the close of our workshop, we envisaged a future where multiple systems employing biohybrid approaches are combined to form a higher-level biohybrid system, able to harness the advantages of collective intelligence. Artificial intelligence (AI), too, will enable engineered systems to quickly interact with animals (Papaspyros et al., 2024). For an engineered system (e.g. a robot) to respond to an animal's behaviour, it has to be able to accurately detect and identify the animal (Mitterwallner et al., 2024), as well as interpret its relevant behaviours through computer vision (Chen et al., 2023; Ng et al., 2022) or other types of sensory data (Szenicer et al., 2022). Many behaviours can be inferred to some extent by simple proxies, such as movement speed or direction (e.g. an animal moving rapidly away from a drone is probably fleeing), but the finer scale, more subtle behavioural recognition, and across diverse environments is still a major challenge (Kholiavchenko et al., 2024; Li et al., 2023). AI may offer a solution here, continuous monitoring

of animal behaviour by AI may not only enable precise detection of behavioural events for individuals but also, when these data are 'joined up,' quantify the state of the planet, from the ground up: sensing locally and integrating information in a hierarchy of computing nodes. Existing sensors and actuators might be connected to a network, like the internet, and algorithms/models may connect these sensory data and yield some form of agent policy acting on the world, both locally and globally (even in the future spanning the entire planet). The planet's 'brain' can then be used in all three proposed themes, to learn about the natural world and provide services (both information and actuation), representing the far endpoint of a full integration.

With AI systems developing at an accelerating pace, we should highlight the socioeconomic pressures that affect the evolution of such systems. We will see accelerated developments of biohybrid systems only when they affect factors that are part of the economic models of policy-makers or promise significant commercial impact. Hence, biohybrid systems we expect to see soon in real-world applications will focus on improving the lives of humans: it will likely be related to agriculture, conservation and pest control. Looking into the future, the organization of such a globalized biohybrid system could be centralized, decentralized or something in between; however, the ethics of such a system will be challenging to work out. The animal behaviour community should have an active role in the gradual steps to be taken towards this development, enabled by central aspects of behavioural ecology (for a detailed review on the practical integration of the two fields into 'machine behaviour' see Rahwan et al., 2019). For this development, a strong interdisciplinary community network, which can be created and sustained through interdisciplinary events such as our ASAB workshop, is crucial. Another way to bridge the two fields is, for example, the publication of annotated data sets; this relatively low time and cost practice can provide a rich resource for engineers to develop algorithms that address real-world challenges, fuelling in turn the availability of cutting-edge tools for the processing and analysis of large quantities of collected data by biologists (Naik et al., 2024). Thus, we encourage animal behaviour scientists to find partners in engineering research groups interested in biohybrid technologies to discuss how both sides can benefit from such collaborations.

Author Contributions

A.L.J. Burns: Writing - review & editing, Methodology, Investigation, Conceptualization. A.J. King: Writing - review & editing, Writing - original draft, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. B.R. Costelloe: Writing - review & editing, Methodology, Investigation, Conceptualization. C.C. Ioannou: Writing - review & editing, Methodology, Investigation, Conceptualization. D.W.E. Sankey: Writing - review & editing, Methodology, Investigation, Conceptualization. D.M. Scott: Writing - review & editing, Methodology, Investigation, Conceptualization. D. Strömbom: Writing - review & editing, Methodology, Investigation, Conceptualization. F. French: Writing - review & editing, Methodology, Investigation, Conceptualization. G. Polverino: Writing - review & editing, Methodology, Investigation, Conceptualization. J.E. Herbert-Read: Writing - review & editing, Methodology, Investigation, Conceptualization. J. Hoitt: Writing – review & editing, Methodology, Investigation, Conceptualization. M. Papadopoulou: Writing review & editing, Writing - original draft, Visualization, Project administration, Methodology, Investigation, Conceptualization. M. Ball: Writing - review & editing, Methodology, Investigation, Conceptualization. M.A. Clark: Writing – review & editing, Methodology, Investigation, Conceptualization. M. Fele: Writing -

review & editing, Methodology, Investigation, Conceptualization. **M.K. Heinrich:** Writing – review & editing, Methodology, Investigation, Conceptualization. **P. Bartashevich:** Writing – review & editing, Methodology, Investigation, Conceptualization. **S. Hauert:** Writing – review & editing, Methodology, Investigation, Conceptualization. **S.R. Matchette:** Writing – review & editing, Methodology, Investigation, Conceptualization. **V.H. Sridhar:** Writing – review & editing, Methodology, Investigation, Conceptualization. **T. Landgraf:** Writing – review & editing, Methodology, Investigation, Conceptualization. **T.T. Vo-Doan:** Writing – review & editing, Methodology, Investigation, Conceptualization. **V. Chiara:** Methodology, Investigation, Conceptualization. **V. Trianni:** Writing – review & editing, Methodology, Investigation, Conceptualization.

Declaration of Interest

The authors declare there are no conflicts of interest.

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12

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