Neuroscience and Biobehavioral Reviews 155 (2023) 105428

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Play behavior in ectothermic vertebrates

Vladimir Dinets

Psychology Dept., University of Tennessee, Knoxville, USA

ARTICLE INFO

Keywords:
Amphibian
Crocodile
Fish
Lizard
Ray
Reptile
Shark
Snake
Turtle

ABSTRACT

Until a few decades ago, play was considered a behavior unique to birds and mammals. Although play in other vertebrates is still a neglected research subject, data on it has been slowly accumulating, and are reviewed here. Now we know that animals as diverse as stingrays, cichlid fishes, monitor lizards, softshell turtles, and crocodiles can be unexpectedly playful. This knowledge has implications to broader theoretical problems, but much more research attention is needed to utilize its potential.

Ectothermic ("cold-blooded") vertebrates include animals traditionally known as "reptiles", "amphibians" and "fishes", although at least two of these groups are not monophyletic (Fig. 1). They vastly outnumber endothermic ("warm-blooded") vertebrates (birds and mammals, although note that a few species of fish and one species of sea turtle can be temporarily endothermic, see below): there are currently over 55,000 species of them, including ~12,000 reptiles (mostly squamates, with just 363 species of turtles, 30 of crocodylians, and 1 of tuatara), ~8600 amphibians, and over 33,000 fishes (of which 118 are jawless fishes, ~1100 are cartilaginous fishes, and the rest are bony fishes), compared to just over 10,000 species of birds and 6649 of mammals (Uetz, 2022; AmphibiaWeb, 2023; Fishbase, 2023; Lepage, 2023; Mammal Diversity Database, 2023). Many species are captive-bred and/or maintained in captivity, and knowledge of their play behavior is important for optimizing habitat enrichment, training and well-being. However, their behavior in general, and play behavior in particular, have received much less attention by researchers than those of endotherms: there are thousands of research papers on play in mammals, and hundreds on play in birds, but ~40 on play in all ectothermic vertebrates (Table 1). The first work to discuss play in ectotherms in general was by Fagen (1981); the only review of play behavior in all ectothermic vertebrates was by Burghardt (2005) with a brief update by the same author (Burghardt, 2015). A few more papers have appeared in recent years, but most reports still come from "grey literature", personal communications, amateur videos and the like.

Why so little interest? Behavioral research has an unhealthy focus on mammals and birds (see discussion in Doody et al., 2021) due to a combination of objective and subjective reasons. The natural behavior of many ectotherm taxa is difficult to observe to begin with, as they are often small, secretive, and/or inhabit deep or turbid waters, subterranean or otherwise enclosed/inaccessible habitats; an overwhelming majority of studies of ectotherm behavior are conducted in captivity where full diversity of an animal's behavior might not be exhibited (Doody et al., 2013). Many mammals (particularly primates) and virtually all birds rely heavily on visual and acoustic communication, while reptiles and amphibians often use primarily chemical signaling, and some of the most behaviorally complex fish taxa can communicate via electric signals, making their social life much more difficult to observe (Rivas and Burghardt, 2002). Finally, play behavior in ectotherms is objectively less common than in endotherms, (see below), and its rarity made it much easier to claim that all reports of play in ectothermic vertebrates are anthropomorphic misinterpretations of other behaviors.

It is well known that humans are less likely to recognize ectotherms as being capable of complex or human-like behavior, and tend to think of them as dumb, an attitude first noted (but also manifested) by Darwin (1845). That creates a lot of skepticism whenever an observed behavior of an ectothermic vertebrate is interpreted as play. A behavior automatically considered play in a dog would most likely be interpreted as something else if observed in a frog. In fact, until the last few decades play was considered unique to mammals and birds, and many cases of play behavior were discounted due to this dogma (Burghardt, 2011). For example, Fagen (1981) dismissed all reports of play in reptiles, stating that juvenile reptiles behave exactly like adults, while Beach (1945)

E-mail address: dinets@gmail.com.

https://doi.org/10.1016/j.neubiorev.2023.105428
Received 17 October 2022; Received in revised form 12 September 2023; Accepted 16 October 2023

explained away playful leaping in needlefishes as parasite removal despite total lack of supporting evidence, and that explanation kept being repeated over and over for over half a century.

How do we know if what we see is play behavior? To answer this question, we need a universally accepted definition of play behavior and precise procedures for distinguishing between play and non-play. Virtually all studies of play behavior in *endothermic* vertebrates don't deal with this question at all, simply assuming that any behavior that resembles play in humans is also play. On the other hand, studies of play in ectothermic vertebrates and invertebrates have for decades struggled with the burden of proving that observed behavior is play and not something else, which was nearly impossible due to lack of universally accepted definitions and criteria.

The only way to deal with this problem is to develop objective criteria for accepting an observed behavior as likely being play, and to apply these criteria to all taxa, no matter how far removed from humans in the tree of life. This is not an easy task. In recent years, the five criteria formulated by Burghardt (2005) have been generally accepted, with an understanding that a behavior might not satisfy all five but potentially still be play:

1. The performance of the behavior is not fully functional in the form or context in which it is expressed; that is, it includes elements, or is directed towards stimuli, that do not contribute to current survival.
2. The behavior is spontaneous, voluntary, intentional, pleasurable, rewarding, reinforcing, or autotelic (done for its own sake).
3. It differs from the "serious" performance of ethotypic behavior structurally or temporally in at least one respect: it is incomplete (generally through inhibited or dropped final element), exaggerated, awkward, or precocious; or it involves behavior patterns with modified form, sequencing, or targeting.
4. The behavior is performed repeatedly in a similar, but not rigidly stereotyped, form during at least a portion of the animal's ontogeny.
5. The behavior is initiated when the animal is adequately fed, healthy, relaxed, and free from stress (e. g. predator threat, harsh microclimate, social instability) or intense competing systems (e. g. feeding, mating, predator avoidance).

This definition does not completely eliminate subjectivity (a "seemingly nonfunctional" behavior might still be functional in a way unknown to the observer; the animal's perception of the setting cannot be precisely known), but it is the only existing set of criteria for distinguishing play from non-play that can be used in studies of animals.

Other proposed definitions of play behavior were all developed exclusively for humans; they are even more subjective and pretty much useless for research in other taxa. Consider, for example, the seminal definition by Huizinga (1938): "Summing up the formal characteristic of play, we might call it a free activity standing quite consciously outside 'ordinary' life as being 'not serious' but at the same time absorbing the

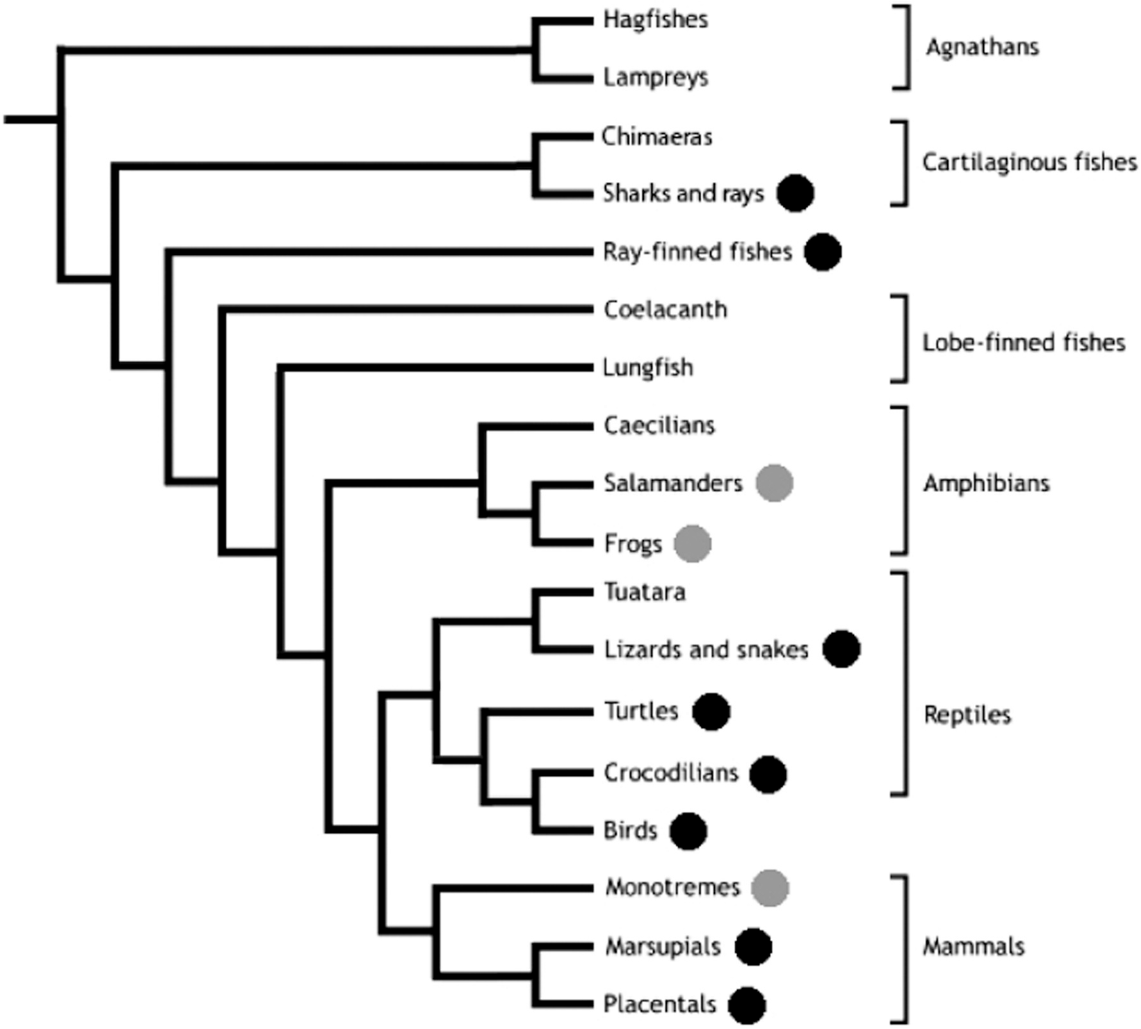

Fig. 1. Simplified phylogeny of extant vertebrates. Circles at the branch tips indicate known presence of play behavior (black circles – at least 5 reports, grey circles – less than 5 reports).

Table 1
Scientific literature on play in ectothermic vertebrates. Types of play as defined in Burghardt and Pellis (2019).

Taxa	Locomotor play	Object play	Social play
Cartilaginous fishes	Burghardt (2005)	Burghardt (2005); Kuba et al. in prep.	
Bony fishes	Khokhlenko (1959); Klausewitz (1966);Fagen (2017)	Holder (1892);Gudger (1944);Ladiges (1954); Meder (1958); Meyer-Holzapfel (1960);Burghardt (2005);Burghardt et al. (2014);Eisenbeiser et al. (2022)	Burghardt (2005); Eisenbeiser et al. (2022)
Amphibians	Burghardt (2005, 2015)	Burghardt (2005)	Hurme et al., 2003
Squamates	Khandakar et al. (2020)	Proctor (1928);Hill (1946);Burghardt et al. (2002);Burghardt (2005);Barabanov et al., (2015, 2019); Kane et al. (2019); Doody et al. (2021)	Cooper (1971); Burghardt (1982); Kramer and Burghardt (1998); Greenberg and Hake (1990); Burghardt (2005); Doody et al. (2021);Brooks and Burghardt (2023)
Turtles		Borodyak (1948); Burghardt et al. (1996); Mann and Mellgren (1998);Krause et al. (1999);Burghardt (2005)	Burghardt et al. (1996);Burghardt (2005);Doody et al. (2021); Mo (2020); Brooks and Burghardt (2023)
Crocodylians	Burghardt (2005);Dinets (2015)	Lazell and Spitzer (1977);Burghardt (2005);Augustine et al. (2015);Dinets (2015)	Dinets (2015)

player intensely and utterly. It is an activity connected with no material interest, and no profit can be gained by it. It proceeds within its own proper boundaries of time and space according to fixed rules and in an orderly manner. It promotes the formation of social groupings that tend to surround themselves with secrecy and to stress the difference from the common world by disguise or other means.".

Human psychologists seemingly have a much easier task separating play from non-play, but even they have not found a universal methodology for doing so, and the term “play” is used in very different ways by different authors. For example, an influential (if widely criticized) book by Berne (1964) used the terms “play” and “games” for all kinds of social roles and interactions.

Fagen (1981) defined three kinds of play behavior: locomotor, object and social play. These are not mutually exclusive, and many instances of play are a combination of all three kinds. A particularly contentious issue has been the interpretation of object play, since any manipulation of an object can alternatively be interpreted as a misguided feeding attempt. Just how long does a tortoise have to keep playing with a rubber ball before we can agree that it’s not trying to eat it? But what we already know about sensory abilities of ectotherm vertebrates makes it certain that it takes them seconds at the most to distinguish between edible and non-edible objects, and that they are often superior in that ability to most endotherms (see, for example, Halpern and Frumin, 1979; Grigg and Kirshner, 2015; Rowland et al., 2015; Kotrschal, 2000). Moreover, these two interpretations are not mutually exclusive: human infants often bite and mouth balls and other objects, and routinely play with food.

Non-functionality is the characteristic most often used in definitions of play, but it is very difficult to demonstrate; moreover, play might actually be functional in few, some, or most cases. To understand Burghardt’s requirement of the behavior in question being “seemingly nonfunctional”, we have to remember that functionality of play is still a controversial subject in human psychology and a largely hypothetical one in animal psychology. It is known from some studies (see, for example, Zhang et al., 2020) and everyday experience that some kinds of play can facilitate learning and physical development, and improve health and general well-being, but this certainly isn’t true for all behaviors routinely called “play” in humans, and is also extremely difficult to demonstrate in animals, so most such claims are never proven (Biben, 1998). Indeed, the difficulties in defining play, interpreting behavior, and experimentally depriving animals of play have led to suggestions that we’ll forever be limited to only circumstantial evidence of play functionality (Caro, 1988). To complicate matters, it appears that different kinds of play can provide different fitness benefits, often delayed, complex and counterintuitive, and are subject to different selective pressures and evolutionary mechanisms (Smaldino et al., 2019; Nunes and Montemayor, 2023; Pellis et al., 2023).

One particularly contentious case is the so-called precocious behavior: immature animals engaging in behaviors that are normally used by adults and are reproduction-related. A well-known example is play fighting, but “play mating” and “play courtship” are also very common. Fagen (1981) did not consider such behavior true play, while Williams (1991) claimed that all play is essentially precocious behavior. More recently, precocious behavior is usually considered play, at least in birds and mammals (see discussion in Burghardt, 2005).

As imperfect as Burghardt’s criteria are, they are the best we have, and might never be substantially improved upon. They helped change researchers’ approach to observations of play in ectotherms, and helped detect play in animals that nobody would consider capable of it just a few decades ago, such as octopuses, spiders, and paper wasps (Dapporto et al., 2006; Pruitt et al., 2012; Kuba et al., 2014). Thanks to Burghardt’s work, play researchers have generally accepted the existence of play in ectotherms as a proven fact (see, for example, the recent review by Pellis and Pellis, 2021), and no claims to the contrary have been made in play literature in recent years. Unfortunately, this is not as widely known to scientists outside the field of play research, leading to loss of valuable observations and study opportunities.

Below I review known cases of ectothermic vertebrates behaving in ways that match Burghardt’s criteria, resemble behavior generally considered play in humans, and cannot be immediately categorized as other known forms of behavior. I will use the term “play” rather than “play-like behavior” or any such construct because “play” is a convenient term, and its imperfections are widely understood by scholars of animal behavior.

Many of the observations described below come from “grey literature” or even social media. Using secondary and anecdotal references was unavoidable because original peer-reviewed studies of play behavior in ectothermic vertebrates are rare and do not provide an adequate picture of its phylogenetic distribution and variability.

1. Cartilaginous fishes

Animals colloquially known as “fish” belong to three extant groups: (1) Agnathans (hagfishes and lampreys), an ancient clade very different anatomically and physiologically from other vertebrates; (2) Chondrichthyes (cartilaginous fishes), which include chimaeras, sharks and rays; and (3) Osteichthyes (bony fishes), which include more than a half of all living vertebrate species. All other living vertebrates (amphibians, reptiles, birds and mammals, collectively known as Tetrapoda) are descendants of one lineage of bony fishes (Fig. 1). Some pelagic fishes are known to become temporarily endothermic while swimming (Wegner et al., 2015).

Not much is known about the behavior of lampreys, hagfishes and chimaeras (most of which are deepwater species), but some sharks and rays have recently been found to exhibit unexpectedly complex behavior, and many researchers now informally call certain species “intelligent”. Manta rays (*Manta* spp.) are among the few animals that have passed the so-called mirror test, generally considered a robust test of self-awareness (Ari and D'Agostino, 2016, although see Gallup and Anderson, 2018). Reticulated freshwater stingrays (*Potamotrygon falkneri*) can use tools (Kuba et al., 2010) and exhibit social learning (Thonhauser et al., 2013). And at least some sharks and rays are now known to play. Great white sharks (*Carcharodon carcharias*) were observed by E. Ritter to play with prey, non-prey animals, or human-provided food items (Burghardt, 2005); indeed, guides conducting cage dives to watch great white sharks in South Africa observe apparent play with floats and other objects a few times per year (John Milne pers. comm.).

Sharks of many species would repeatedly leap out of the water, often in a spectacularly acrobatic manner; such behavior is often considered play in cetaceans, but unlike in cetaceans, leaping in sharks doesn't appear to have communicative functions (Burghardt, 2005). Sometimes sharks leap to dislodge commensal sharksuckers (*Echeneis* spp.) (Brunnschweiler, 2006), but this doesn't explain all leaping. Fast-swimming pelagic sharks have few, if any, ectoparasites (Gilbert, 1967) that they could potentially try to escape by leaping.

Freshwater stingrays (*Potamotrygon* spp.) play with small balls and would even fight for access to them; adults play more often than juveniles (Kuba et al. in prep., cited with permission). Many rays will readily interact with humans and other species in a playful manner. At the famous Stingray City on Grand Cayman Island, where many generations of southern stingrays (*Hypanus americanus*) have been habituated and have by now significantly altered their behavior (Shackley, 1998), certain individuals are so "friendly" that they can be lifted out of the water, held in place for minutes at a time, and even flipped over (pers. obs.). In decades of "stingray tourism", no case of the rays using their poisonous barb against tourists or guides has been recorded, even though the same species readily uses the barb in self-defense if threatened and is a frequent cause of hospitalizations elsewhere (Gilbert, 1967). Cownose rays (*Rhinoptera bonasus*) commonly kept in touch tanks in zoos and oceanariums are usually indifferent to humans, but one subadult that lived in Turtleback Zoo in New Jersey would approach a particular child and spend up to ten minutes rubbing against her hands, splashing, and apparently soliciting belly tickles (pers. obs.). A manta ray (*Manta* sp.) in Osaka Aquarium would repeatedly ride on the back of a whale shark (*Rhincodon typus*) kept in the same tank (pers. obs.), although this behavior could also be interpreted as energy saving or reproduction-related rather than playful.

2. Bony fishes

Our appreciation of the complexity of fish behavior has grown exponentially in recent years (see overview in Balcombe, 2016). However, although play has been observed in numerous species of bony fishes, research on their play behavior has been lagging so badly that it still barely exists. Burghardt (2005) remains the most comprehensive review; a more recent literature review by Eisenbeiser et al. (2022) reported no new studies except their own.

Extant bony fishes belong to two major lineages: lobe-finned fishes (Sarcopterygii, 8 species only, but all amphibians, reptiles, birds and mammals also belong to this clade), and ray-finned fishes (Actinopterygii) (Fig. 1). Observations of play behavior are scattered all over the phylogenetic tree of ray-finned fishes, from some taxa traditionally considered "ancient" and "primitive", such as sturgeons (Acipenseridae), to the "advanced" groups that have diversified more recently, such as cichlids (Cichlidae).

The earliest published examples of play behavior in fishes were by Holder (1892), who described needlefishes (*Strongylura* spp.) repeatedly jumping over floating objects and even other animals such as turtles; this behavior is common and has been subsequently noted by many researchers. In addition to needlefishes, leaping over objects is known in related (halfbeaks, Hemiramphidae) and unrelated (silversides, Atherinidae, and many others) fish taxa (Gudger, 1944). Even more common and widespread is simple leaping out of the water; some species such as Atlantic tarpon (*Megalops atlanticus*), striped mullet (*Mugil cephalus*), and silver carp (*Hypophthalmichthys molitrix*) are particularly well known for frequent leaping. Six other explanations have been proposed for leaping behavior (see overview in Stell, 2018): ectoparasite removal, predator avoidance, respiration, predation, crossing barriers, and intraspecific signaling. Some of these explanations are supported by evidence in certain cases, but leaping in most species remains unexplained. For many decades, this behavior was considered to be a form of ectoparasite removal (Beach, 1945), but, for example, captive-bred sterlets (*Acipenser ruthenus*) kept in tanks would leap despite being completely parasite-free (Khokhlenko, 1959). Gulf sturgeons (*Acipenser oxyrinchus*) likely use leaping for acoustic communication during the breeding season (Sulak et al., 2002), but sturgeon of this and other species also leap outside the breeding season (Khokhlenko, 1959). Leaping behavior in Trinidad guppies (*Poecilia retiuclata*) and paddlefish (*Polyodon spathula*) has been found to be spontaneous and lacking any obvious purpose (Soares and Beirman, 2013; Stell, 2018). Some species of minnows (Cyprinidae) are now known to enjoy being thrown into the air by hand (Klausewitz, 1966), showing that leaping might be a pleasant experience. Even very

Table 2
Selected online videos of play behavior by ectothermic vertebrates.

Subject	Posted by	URL
Juvenile oceanic sunfish (*Mola mola*) leaping	Newport Whales	https://twitter.com/NewportWhales/status/1349083820583124992?fbclid=IwAR3y-B-Iq1FDvD1YiioQ35qsauc-is9P8qG61dV2cxc_2nn-7fYmCDY2HBw
Juvenile savannah monitors (*Varanus exanthematicus*) play-wrestling	Dean Cheetham	https://www.facebook.com/dean.cheetham.3/posts/10220634185636636
Komodo dragon (*V. komodensis*) apparently playing with a turtle shell	RMVideos	https://www.youtube.com/watch?v=M2h0ZEi65W8
Bearded dragon (*Pogona vitticeps*) playing chase with a dog	Meo Madeley	https://www.youtube.com/watch?v=kGS5gFjjMgU&t = 69 s
Bearded dragon playing tug-of-war with a dog	Kelsey Looney	https://www.youtube.com/watch?v=V-YtK3jIr6Y
Argentine black and white tegus (*Salvator merianae*) playing with objects	Winston the Tegu	https://www.facebook.com/reel/1160655918128023?fs=e&s = TIeQ9V https://www.facebook.com/reel/775040730587700?fs=e&s = TIeQ9V https://www.facebook.com/reel/1221840411943095?fs=e&s = TIeQ9V https://www.facebook.com/reel/536086331621984?fs=e&s = TIeQ9V
Multiple species of lizards playing with objects	Tom Crutchfield	https://www.youtube.com/watch?v=J4Q3Q2IMn3g
Central American boa (*Boa imperator*) apparently using its tongue to play with a feather	Robert Hatfield	https://www.facebook.com/groups/1235459976500320/posts/1380318108681172/
Ball python (*Python regius*) playing with a ball	Discover Snakes	https://www.instagram.com/p/Bu2AqHwHB4J/?hl=en
Red-eared slider (*Trachemys scripta*) playing with rocks	Jessica Lodwick	https://www.facebook.com/groups/439160636196535/posts/1890282384417679/
Red-eared slider playing chase with a domestic cat	Metocco	https://www.youtube.com/watch?v=N22–9h4r8No
African spurred tortoise (*Geochelone sulcata*) playing ball with a dog	Andrew Atwood	https://www.youtube.com/watch?v=HWvpP8kZLdc
Marginated tortoise (*Testudo marginata*) playing ball with a dog	Rudy Janssens	https://www.youtube.com/watch?v=dHAlMvYuPvg

slow-moving fish, such as juvenile oceanic sunfishes (*Mola mola*), seem to enjoy leaping (see Table 2). The purpose of leaping has been discussed in scientific as well as non-scientific literature, and play is becoming an increasngly common interpretation (Dobson, 2010; Fagen, 2017).

Playing with objects appears to be widespread among fish but is often difficult to separate from feeding attempts, especially since much of it involves playing with food. Not surprisingly, published (as opposed to anecdotal) observations often report play with inedible objects. Sturgeons, particularly sterlets, are attracted to shiny objects and often push them around, even though they normally feed on benthic invertebrates which are not shiny (Ladiges, 1954). Two interesting reports by aquarium curators are cited by Burghardt (2015): Inge Illich observed grey triggerfish (*Balistes carolinensis*) carrying various objects and manipulating golden bracelets on her hands, while Sandy Trautwein observed surgeonfish of two species (*Paracanthurus hepatus* and *Acanthurus thompsoni*) repeatedly gulping air at the surface, releasing bubbles near the bottom of the tank, and chasing them back to the surface, essentially making their own toys. Like tadpoles, fishes in tall aquariums can repeatedly ride air bubble streams through water columns (G. M. Burghardt, pers. comm).

One of the best-documented cases of object play in fish is of the white-spotted cichlid (*Tropheus duboisi*). Some captive individuals of this species would for years interact with a bouncing aquarium thermometer, pushing it repeatedly (Fig. 2). Burghardt et al. (2014) studied this behavior in three male cichlids and found that it is best interpreted as play, as alternative interpretations were contradicted by evidence: thermometer attacks did not resemble feeding or courtship behavior of the white-spotted cichlid, while the results of lag sequential analysis and general patterns of occurrence were incompatible with redirected aggression in at least 2 out of 3 observed individuals. Notably, the fish only attacked thermometers when unstressed and kept in tanks with few or no other fish, suggesting that this behavior was caused by sensory deprivation, which is known to stimulate play in many other species (Burghardt, 1984).

Eisenbeiser et al. (2022) conducted a study of fishes chasing laser pointers of various colors. Out of 66 species they tested (in fish tanks), over 80% showed interest in pointers, with red being the most popular color. In 15 species the response lasted more than 5 s (by which time they were likely aware that the pointer was not edible, see above), and some species showed interest in the pointer for up to two weeks after first presentation. The authors consider play and attempted predation as the most likely interpretations of this behavior but note that the one of the species with high response to the pointer was the rainbow shark (*Epalzeorhynchos frenatum*), which is not a true shark but a small herbivorous minnow unlikely to chase the pointer in a predation attempt.

One family in which playing with objects is particularly common and spectacular is freshwater elephantfishes (Mormyridae). These weakly electric fishes have trunks that they use to manipulate objects, and many appear to enjoy playing with balls, twigs and other inedible objects placed in their tanks, pushing them around, balancing on their snouts, or repeatedly bringing them to the surface and dropping to the bottom. This was first reported by Meder (1958) and extensively reviewed by Meyer-Holzapfel (1960), who found play to be much more likely than any alternative interpretation of the behavior (the rejected interpretations included: singular aberration, scratching, redirected feeding, courtship or aggressive behavior, nest building, and nonsexual social interaction). The latter author also reported that some individuals would play in this way with particular conspecifics (with two individuals taking turns moving each other around) and suggested that such social play might be more common in the wild than in captivity, and that manipulating objects might be just a substitution for playing with conspecifics.

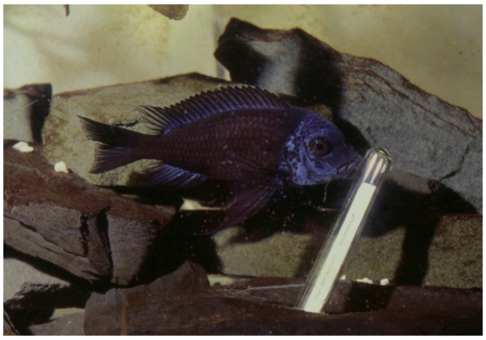

Fig. 2. A white-spotted cichlid (*Tropheus duboisi*) playing with a thermometer that would immediately right itself. Photo by Ann Hawthorne from Burghardt et al. (2015).

As for play with edible objects, one of the most remarkable observations was by Jarmer (1928), who observed two pikes (probably *Esox lucius*) repeatedly taking turns catching a small fish and “spitting” it at one another. At some point the small fish, still alive, was abandoned and the exchange continued with another small fish.

There is some anecdotal evidence of chasing and teasing play in fishes, particularly in cichlids, but, although such behavior is occasionally noted in literature (i. e. Eisenbeiser et al., 2022), there are no published studies focused on it. James Murphy (cited in Burghardt, 2005) observed and videotaped a blunthead cichlid (*T. moorii*) that lived in a large communal tank. It would repeatedly approach a larger, but slower, male blue mbuna (*Labeotropheus fulleborni*) and perform a lateral display that would elicit a brief chase by the latter. These provocations continued for days, and as Burghardt notes, “this behavior, seen in a dog or monkey, would unhesitantly be labeled teasing play”.).

Juvenile coho salmon (*Oncorhynchus kisutch*) of both sexes engage in rolling behavior reminiscent of nest-building by adult females. This behavior is not feeding-related (as shown by analyzing stomach contents), but is remarkably similar to precocious sex play found in mammals and turtles (Nielsen, 1990; Burghardt, 2005).

3. Amphibians

Extant amphibians belong to three orders: Anura (frogs, the largest group), Urodela (salamanders), and Apoda (caecilians). The latter are subterranean or aquatic and very little is known about their behavior, but many species of frogs and salamanders are common in pet trade, and some are widely used as model organisms. Despite that, observations of play behavior in amphibians are outstandingly rare.

Tadpoles of Vietnamese mossy frog (*Theloderma corticale*) were reported by K. Zippel to repeatedly ride a column of rising air bubbles in their tank. This behavior was replicated and videotaped by Burghardt (2015), who then replaced air with helium and found that the behavior persisted and thus cannot be interpreted as respiration related. A similar behavior has been observed in axolotls (neotenic larvae) of Mexican mole salamander (*Ambystoma mexicanum*) in tanks with horizontal airstreams (Burghardt, 2005).

Blue (*Dendrobates azureus*) and green (*D. auratus*) poison dart frogs apparently engage in play fighting and in jumping over each other; these behaviors have been interpreted as being related to territorial defense or courtship (Hurme et al., 2003). Burghardt (2015) reproduced and videotaped them, and found no evidence supporting either interpretation, but noted that both behaviors were most common after feeding and in benign conditions, which supports interpreting them as play. Blue poison dart frogs were also reported by E. Bryant-Cavazos to push around dice placed in their enclosures (Burghardt, 2005).

4. Squamates

Extant animals colloquially known as “reptiles” belong to two clades that have diverged more than 250 mya: Archosauromorpha and the Lepidosauromorpha (Colbert et al., 2001). The former include crocodylians, birds (living representatives of dinosaurs), and, according to most recent data (Schoch and Sues, 2015), also turtles, while the latter include squamates (lizards and snakes) and their sister clade that today includes only one species, the tuatara (*Sphenodon punctatus*) of New Zealand. There is no evidence of play behavior in the tuatara, and no such evidence for many well-studied species of squamates (but such species are a tiny minority of all squamates since we know little or nothing about the behavior of most taxa).

One group of squamates for which play behavior is well documented is the monitor lizards (*Varanidae*), particularly Komodo dragons (*Varanus komodoensis*). It was first reported by Proctor (1928) and later by Hill (1946), who observed a captive male dragon playing with his keeper's shovel by dragging it over stones and apparently trying to make as much noise as possible. Burghardt et al. (2002) observed a captive female dragon for a few years. She would repeatedly and noisily push around a bucket, pull notebooks and other objects from her familiar keeper's pocket and carry them around without chewing on them, and even play tug-of-war and keep-away with the keeper. A set of trials showed that her preferred toys were large plastic rings and sneakers. Her play behavior was remarkably similar to that of dogs, particularly if she played with a shoe and the video recordings were replayed at double speed. Other trials definitively showed that the animal treated her toys differently from potentially edible objects, and stopped playing with the keeper if there was food or objects smelling like food in the enclosure, switching instead to typical food-defending behavior.

Manrod (2003) studied the behavior of captive hatchlings of black-throated monitor (*V. albigularis*). The animals were presented with plastic ball and tube containing food; food in the ball could not be obtained while food in the tube could be. Initially the monitors reacted to both objects in similar ways, but as they learned that food in the ball could not be retrieved, they began switching from predatory behavior (biting) to play (nudging and rolling). This behavior was remarkably similar to predatory play observed in domestic cats.

Juvenile savannah monitors (*V. exanthematicus*) engage in play-wrestling (see Table 2) and also in precocial sexual behavior, which is usually considered play in mammals (Bayless, 1994; Burghardt, 2005). Play behavior has been reported in captive adult blue-spotted (*V. macraei*) and juvenile green (*V. prasinus*) tree monitors, which would tear off leaves, carry them around and then shred into pieces or wipe against rocks (Kane et al., 2019). Wild yellow monitor (*V. flavescens*) was observed swimming back and forth in a vertical position for up to three minutes at a time, an unusual behavior interpreted by the observers as play (Khandakar et al., 2020). There are multiple videos of monitors playfully sticking their heads into boxes, sea turtle shells, etc., and carrying them around (Doody et al., 2021), and of a black-throated monitor playing with a plastic toy (G. M. Burghardt pers. comm.).

Evidence of play in other lizards (first overviewed in Burghardt, 2005) is limited and mostly anecdotal. It currently includes reports and videos of captive lizards, including herbivorous species such as rhinoceros iguana (*Cyclura cornuta*), playing with objects. Many lizards show positive response to enrichment of their habitat with diverse objects (Bashaw et al., 2016; Howard and Freeman, 2022). Schwing and Wein (2016) noted that captive Argentine black and white tegus (*Salvator merianae*) spent more time investigating non-edible novel objects than edible ones, and argued that such behavior is a form of play. Some individuals of this species are particularly fond of playing with various objects (see links to videos, Table 2). Turner's thick-toed geckos (*Chondrodactylus turneri*) played with objects in weightless conditions of an orbiting spacecraft and did it more often than on Earth (Barabanov et al., 2015, 2019).

Another reported form of play behavior in lizards is precocious play: juveniles performing territorial and courtship displays (such as head-bobs) that are functional only in adults. In the species of lizard on which most studies of lizard behavior have been focused, the Carolina anole (*Anolis carolinensis*), headbob displays are territorial in adults, but also commonly performed by juveniles and even hatchlings, and resemble numerous examples of play in juvenile birds and mammals (Cooper, 1971; Greenberg and Hake, 1990; Burghardt, 2005). Juvenile chameleons (Chameleonidae) sometimes play-wrestle (Burghardt, 1982).

There are YouTube videos of pet inland bearded dragons (*Pogona vitticeps*) playing chase and tug-of-war with domestic dogs and a wild crow (*Corvus* sp.) in indoor and outdoor settings (Doody et al., 2021; Brooks and Burghardt, 2023; see Table 2 for links to some of the videos). Unfortunately, these videos usually do not provide much context, so it is unknown how regular these behaviors are and in which circumstances they are more likely to be exhibited. On the other hand, it is possible that many instances of play behavior are too subtle to be recognized.

In the same review (2005), Burghardt noted that evidence of play in snakes is more limited. He suggested that knotting behavior, in which snakes form knots with their bodies, might sometimes be a form of play, and cited a pers. comm. by Dan Mulcahy, who observed a captive gopher snake (*Pituophis catenifer*) repeatedly climbing through a cord loop at the top of its cage for no apparent reason. He also cited an unpublished manuscript by David Cundall suggesting that many species of snakes play with water while drinking. There is an amazing video of a subadult ball python (*Python regius*) repeatedly retrieving a ball for its caregiver using its coils in different ways, in an apparent game of ’fetch’, and another one of a Central American boa (*Boa imperator*) seemingly using its tongue to play with a feather (see links in Table 2). Unfortunately, both videos are brief and, again, little further information or context is provided.

5. Turtles

Extant turtles belong to two ancient lineages: side-necked turtles (Pleurodira) and more diverse hidden-neck turtles (Cryptodira). The only published evidence of play behavior in side-necked turtles is a cursory report of a captive mata-mata turtle (*Chelus fimbriata*) occasionally playing with dead fish (Borodyak, 1948). But play behavior in hidden-neck turtles is documented remarkably well (reviewed in Burghardt, 2005).

Burghardt et al. (1996) studied play in captive African softshell turtles (*Trionyx triunguis*). One very old (>50 years) captive male, initially presented with various objects in order to decrease self-harming behavior, began to spend a lot of time (almost a third of all time he was active) manipulating them (nosing, biting, grasping, chewing, pushing, pulling, shaking, or holding down) with his mouth or forelimbs. Different objects were manipulated in different ways (for example, hoops were positioned vertically and then the animal would swim through them), and novel objects were used more often than familiar ones. He would also use a rubber hose to play tug-of-war with a familiar keeper and has reportedly done so for many years. It is usually very difficult to conclusively demonstrate that a behavior is a source of pleasure for the animal (a criteria for play used in many definitions), but this particular turtle provided good evidence: when his tank was being refilled, he ‘would orient toward the hose so that the stream of water flowed over his head. He appeared unsatisfied until he had adjusted the direction of the hose so it was “just right”. When everything was set, he would remain there motionless for some time. That was rather striking giving his usual high rate of activity. When the water was turned off, the turtle rapidly became restless and moved off.” (Burghardt, 2005). Observations on other individuals of the same species showed that they used various objects in very similar manner and played more often when kept in small tanks (Krause et al., 1999) - a pattern also known in rats (Siegel and Jensen, 1986).

Playing with objects has been documented in sea turtles (Cheloniidae), particularly the green sea turtle (*Chelonia mydas*); it has been observed in the wild as well as in captivity (Mann and Mellgren, 1998; Burghardt, 2005). In some cases, the animals would play with a red ball but not with a grey one, or with rough-textured objects but not with smooth ones (Barbara Savitsky and R. I. Mellgren pers. comm. in

Burghardt, 2005). Captive red-eared sliders (*Trachemys scripta*) sometimes play with rocks (see Table 2). There is an anecdotal report of a captive wood turtle (*Glyptemys insculpta*) repeatedly climbing an inclined wooden board and sliding into the water (Burghardt, 2005).

Turtles and tortoises would play with turtles and tortoises of other species (Mo, 2022) and even with other animals. A captive green sea turtle was reported by Bauer et al. (2020) to repeatedly play with a West Indian manatee (*Trichechis manatus*) by riding the manatee, tandem swimming, and touching, with play initiated and terminated by both animals. There are videos on YouTube of pet tortoises (*Testudo* spp., *Geochelone sulcata*) playing ball with dogs, and of a red-eared slider playing chase with a domestic cat (Doody et al., 2021; Brooks and Burghardt, 2023; see Table 2 for links to some of the videos). Burghardt (2005) cited a pers. comm. by Monique Halloy, who observed a pet turtle (*Chrysemys* sp.) repeatedly teasing a dog by surfacing nearby and then diving just as the dog was about to grab it, and a pers. comm. by Barbara Savitsky, who observed a captive loggerhead sea turtle (*Caretta caretta*) that would repeatedly grab the tail of a nurse shark and go for a ride while the shark tried to escape; the same animal also engaged in prolonged bouts of play with plastic balls and foam rings, but never left bite marks on them, indicating that there were no feeding attempts.

Kramer and Burghardt (1998) provided a detailed analysis of courtship-like behavior in juvenile pond turtles (Emydidae) and concluded that it is best interpreted as play. It occurs most often in species practicing the so-called titillation during courtship, but titillation displays by juveniles are simplified, sometimes longer, and can be addressed at inanimate objects, particularly when performed by neonates. Many juveniles seem to have preferred “playmates” for those displays. In rare cases when the display is followed by a mounting, females sometimes mount males. In the case of Florida red-bellied cooters (*Pseudemys nelsoni*) juveniles perform those displays in a way that is apparently ancestral in the lineage rather than species-specific. The authors noted that these characteristics of the behavior were very similar to those of sexual play in juvenile mammals, such as dominant mountings in juvenile ungulates.

6. Crocodylians

Crocodylians are the closest living relatives of dinosaurs (including birds) and extinct flying reptiles. There is growing evidence that their common ancestor was endothermic, and that crocodiles reverted to ectothermy to lower the energy requirements as they evolved into ambush hunters (Grigg and Kirshner, 2015). It is now believed that many non-avian dinosaurs were endothermic (reviewed in Grigg et al., 2022); it is not known if they played but there is one controversial report (Rothschild, 2015) of possible evidence of play behavior in tyrannosaurid dinosaurs, based on the pattern of tooth marks on the bones of ceratopsian dinosaurs.

Crocodylian play behavior was reviewed by Burghardt (2005) and later Dinets (2015). The latter review cites observations of a juvenile American alligator (*Alligator mississippiensis*) repeatedly using slides, a hatchling broad-snouted caiman (*Caiman latirostris*) repeatedly riding a water stream, and of an estuarine crocodile (*Crocodylus porosus*) surfing ocean waves, but most reports are of play with objects. Favorite objects to play with in captivity appear to be jets of water: Lazell and Spitzer (1977) observed an American alligator playing with water dripping from a pipe for at least 45 min, while Heinbuch and Wiegman (2000)) observed juvenile Cuvier’s dwarf caimans (*Paleosuchus palpebrosus*) repeatedly standing on their hind legs under a warm shower. Floating balls and prey items are also frequently played with, with some indications that red or pink objects are preferred: remarkably, two unrelated species – Cuban crocodile (*Crocodylus rhombifer*) and West African dwarf crocodile (*Osteolaemus* cf. *tetraspis*) – were photographed at different locations by Dinets (2015) playing with pink *Bougainvillea* flowers and ignoring other floating flowers and leaves. Captive Cuban crocodiles playing with cinder blocks appeared to choose the ones colored differently from the rest (Augustine et al., 2015).

Social play has also been observed. Juveniles sometimes ride on each other, and in mixed creches younger animals often ride on the backs of older ones (Fig. 3) (Dinets, 2015). A pair of Cuban crocodiles that has been kept together for many years was observed to incorporate back rides (Fig. 4) into the courtship during the mating season; such behavior has never been observed in any Cuban crocodiles or other crocodylians during courtship, so it is not a normal part of courtship behavior (Dinets, 2011, 2015). There are known cases of crocodylians playing with people, in one case repeatedly for many years, and one case of apparent play with a river otter (*Lontra canadensis*) that culminated with a subadult American alligator catching the otter and releasing it unharmed (Dinets, 2015).

7. Discussion

Complex behavior in general, and play behavior in particular, of many ectothermic vertebrates is under-observed, under-recognized, and underreported for a number of objective and subjective reasons (see above). But it also appears that play behavior in ectotherms is truly rare compared to endothermic vertebrates, particularly some mammals such as carnivores and primates. Even researchers particularly interested in the subject, and prepared to notice play if they see it, report it as seldom occurring: Dinets (2015) recorded behaviors that could be interpreted as play only seven times in ~3000 h of observing crocodilians of various species, while Burghardt (2005) has not seen unambiguous play by snakes in many decades of observing them. Why such difference? There is a number of possible explanations (not necessarily mutually exclusive), discussed below.

1. Could it be that all claimed instances of play behavior in ectotherms are simply misinterpretations by observers and/or freak pathological behaviors by a small number of individuals? It is difficult to be absolutely certain because (a) our overall understanding of animals’ motifs and mental condition is inherently limited, (b) a universally applicable definition of play might be impossible to develop, and (c) the same behavior might have completely different mechanism in different individuals, not to mention different species and higher

Fig. 3. A juvenile American alligator (*Alligator mississippiensis*) riding on the back of an older conspecific from a mixed creche. From Dinets (2015).

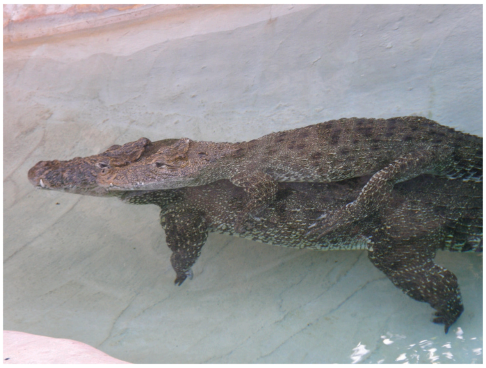

Fig. 4. A female Cuban crocodile (*Crocodylus rhombifer*) riding on the back of her lifetime mate during seasonal courtship. From Dinets (2011).

taxa. Despite these difficulties, at least in some taxa (i. e. monitor lizards) play is diverse, very similar to play in mammals, and well documented by multiple observers and in numerous individuals, leaving little, if any, room for alternative explanations, so the idea that such behavior is limited to endotherms has been disproven beyond reasonable doubt. Now we should focus on documenting play behavior in various taxa and learning from its similarities, as well as differences.

2. One suggestion (Burghardt, 1982) is that animals play more often when they are not constrained by energy budgets; this is known as the Surplus Resource Theory of Play (hereafter SRTP). Endotherms are supposedly less constrained due to higher metabolic rate and energy turnover. This would explain why so many observations listed above were made in captivity rather than in the wild, where most animals have less saturated energy budget. Although observing bias is obvious, it is worth noting that there are only two reports of play-like behavior by Komodo dragons in the wild (Auffenberg, 1981; see also Table 2), even though many of these lizards are habituated to humans and daily observed by tourists and park rangers (pers. obs.). SRTP can also explain why Turner's thick-toed geckos (*Chondrodactylus turneri*) play more often in weightless conditions of an orbiting spacecraft than on Earth where the energetic cost of movement is higher (Barabanov et al., 2015, 2019). One prediction of the SRTP is that juveniles should play more often in species with extended parental care that includes food provision. Such parental care exists in all mammals (although in some species lactation only lasts for a few days) and almost all birds, but food provision for juveniles is very rare in ectothermic vertebrates, being so far known only for some crocodilians, poison dart frogs, caecilians, and cichlids (Balshine, 2012). And, indeed, juvenile mammals play more often than adults, while very limited data suggest that the opposite might be more common in endothermic vertebrates. However, the available data for birds are mixed: juvenile parrots play more often than adults (Bond and Diamond, 2003), but in rheas the trend is reversed (Zeiträg et al., 2023), and in Australian magpies play frequency peaks post-fledging when the birds transition to independent foraging (Pellis, 1981), so it's unclear if the prediction holds. It is also worth noticing that higher energy requirements of endotherms (a mammal needs approximately ten times more food than a crocodylian of the same body mass, see Grigg and Kirshner, 2015) might mean that they could actually be more energy-challenged than ectotherms.
3. Another possible explanation (Burghardt, 2005) is that animals with more flexible, largely learned behavior play more often because play helps the learning process. Indeed, most observations of play behavior in both endotherms and ectotherms seem to be in species that people tend to consider "intelligent", presumably because they are similar to humans in behavioral flexibility and adaptability. It is also possible that people are simply more willing to interpret behavior as play in animals they consider "smart", but it appears that there is true correlation between behavioral complexity/flexibility and the tendency to play. Note that many species mentioned in this review have relatively large and complex brains (for example, elephantfishes have larger relative brain size than humans). It has been shown that bird taxa with larger brains are more likely to play (Kaplan, 2020). It has also been shown that play complexity is higher in birds that take longer to mature and become independent (Bond and Diamond, 2003), but this has never been tested in ectotherms. In mammals, both prevalence and complexity of play are positively correlated with relative brain size at higher taxonomic levels, but not within orders (Iwaniuk et al., 2001).
4. Yet another explanation (Burghardt, 2005) is that mammals and birds are more dexterous and simply have more physical options for play, particularly with objects. That could explain why lizards are reported playing more often than snakes, and why there are no reports of play in legless lizards.

Whatever the explanation(s), the rarity of play in ectotherms is yet another factor preventing research on play behavior in these animals from being considered serious or promising, and its unpopularity, in turn, makes well-documented observations even more scarce. This cycle needs to be broken. Herpetologists and ichthyologists should be prepared to recognize play if they see it, to document it, and to design experiments that would eliminate as many alternative interpretations as possible. Any such observation should be considered a rare and fortunate opportunity to improve our knowledge of a much-neglected area of animal behavior research. One kind of study that is particularly needed is observing the development of play behavior in animals during their growth from newborns/hatchlings through maturity; such observations still exist only for mammals and very few birds. But casual observations are also useful: as they accumulate and involve more taxa, we can get a finer understanding of phylogenetic patterns (Fig. 1) and begin to test correlations with brain size, ontogeny parameters, social structure, and other factors known to influence prevalence and complexity of play in birds and mammals.

Particularly interesting research questions are, of course: (1) are neurological mechanisms of play similar between animals belonging to unrelated groups? (2) does play predictably appear in animals with complex, flexible behavior? (3) if so, why? To answer these questions, we need research on neurology of play in ectothermic vertebrates and invertebrates, possibly using modeling (Smaldino et al., 2019). To date, neurology of play has been extensively studied primarily in rodents (Pellis and Pellis, 2009; see overviews of recent studies in Achterberg and Vanderschuren, 2023 and Cooper et al., 2023).

Studying play in ectothermic vertebrates is difficult, but important for understanding how complex behavior evolves, how brain complexity develops during ontogeny, and how universal are various features of complex brains. It might help us finally understand why play exists and why it is so diverse, and provide other valuable insights for neuroscience and behavioral evolution.

Data availability

No data was used for the research described in the article.

Acknowledgements

I'd like to thank Gordon Burghardt and anonymous reviewers for extensive and thorough help with editing.

References

Achterberg, E.M., Vanderschuren, L.J., 2023. The neurobiology of social play behaviour: past, present and future. Neurosci. Biobehav. Rev. 152, 105319 https://doi.org/10.1016/j.neubiorev.2023.105319.

AmphibiaWeb, 2023. AmphibiaWeb, https://amphibiaweb.org University of California, Berkeley, CA, USA. Accessed 23 April 2023.

Ari, C., D'Agostino, D.P., 2016. Contingency checking and self-directed behaviors in giant manta rays: Do elasmobranchs have self-awareness? J. Ethol. 34, 167–174. https://doi.org/10.1007/s10164-016-0462-z.

Auffenberg, W., 1981. The Behavioral Ecolofy of the Komodo Monitor. University of Florida Press.

Augustine, L., Miller, K., Burghardt, G.M., 2015. *Crocodylus rhombifer* (Cuban Crocodile). Play behavior. Herpetol. Rev. 46, 208–209.

Balcombe, J., 2016. What a Fish Knows: The Inner Lives of Our Underwater Cousins. Scientific American/Farrar, Straus and Giroux.

Balshine, S., 2012. Patterns of parental care in vertebrates. In: Royle, N.J., Smiseth, P.T., Kölliker, M. (Eds.), The Evolution of Parental Care, 2012. Oxford University Press, pp. 62–79.

Barabanov, V., Gulimova, V., Berdiev, R., Saveliev, S., 2015. Object play in thick-toed geckos during a space experiment. J. Ethol. 33, 109–115. https://doi.org/10.1007/s10164-015-0426-8.

Barabanov, V.M., Gulimova, V.I., Berdiev, R.K., Saveliev, S.V., 2019. Individual features of play behavior in thick-toed geckos in weightlessness and normal gravity conditions. Life Sci. Space Res. 22, 38–46. https://doi.org/10.1016/j.lssr.2019.07.002.

Bashaw, M.J., Gibson, M.D., Schowe, D.M., Kucher, A.S., 2016. Does enrichment improve reptile welfare? Leopard geckos (*Eublepharis macularius*) respond to five types of environmental enrichment. Appl. Anim. Behav. Sci. 184, 150–160. https://doi.org/10.1016/j.applanim.2016.08.003.

Bauer, G.B., Deimeke, M., Foltz, A., 2020. Manatee/green sea turtle behavioral interactions: interspecies play? Sirenews 72, 22–24.

Bayless, M.K., 1994. Zur Fortpfanzungsbiologie des Steppenwarans (*Varanus exanthematicus*). Salamandra 30, 109–118.

Beach, F.A., 1945. Current concepts of play in animals. Am. Nat. 79, 523–541. https://doi.org/10.1086/281288.

Berne, E., 1964. Games People Play: The Psychology of Human Relationships. Grove Press.

Biben, M., 1998. Squirrel monkey play fighting: making the case for a cognitive training function for play. In: Bekoff, M., Byers, J.A. (Eds.), Animal Play: Evolutionary, Comparative, and Ecological Perspectives. Cambridge University Press, pp. 161–182. https://doi.org/10.1017/CBO9780511608575.009.

Bond, A., Diamond, J., 2003. A comparative analysis of social play in birds. Behaviour 140, 1091–1115. https://doi.org/10.1163/156853903322589650.

Borodyak, L.M., 1948. МатаМата в ОдесскоМ зоопарке [Matamata in Odessa Zoo]. MOIP Bull. (Biol.) T57, 10–11.

Brooks, H.J.B., Burghardt, G.M., 2023. A comparative review of interspecific social play among nonhuman animals. Neurosci. Biobehav. Rev. 151, 105232 https://doi.org/10.1016/j.neubiorev.2023.105232.

Brunnschweiler, J.M., 2006. Sharksucker-shark interaction in two carcharhinid species. Mar. Ecol. 27, 89–94. https://doi.org/10.1111/j.1439-0485.2005.00052.x.

Burghardt, G.M., 1982. Comparison matters: curiosity, bears, surplus energy and why reptiles don't play. Behav. Brain Stud. 5, 159–160. https://doi.org/10.1017/S0140525X00010979.

Burghardt, G.M., 1984. On the origins of play. In: Smith, P.K. (Ed.), Play in Animals and Humans. Basil Blackwell, pp. 5–41.

Burghardt, G.M., 2005. The Genesis of Animal Play: Testing the Limits. . MIT Press.

Burghardt, G.M., 2011. Defining and recognizing play. In: Pellegrini A.D. (Ed.), The Oxford Handbook of the Development of Play. Oxford University Press, pp. 9–18.

Burghardt, G.M., 2014. A brief glimpse at the long evolutionary history of play. Anim. Behav. Cogn. 1, 90–98. https://doi.org/10.12966/abc.05.01.2014.

Burghardt, G.M., 2015. Play in fishes, frogs and reptiles. Curr. Biol. 25, R9–R10.

Burghardt, G.M., Pellis, S.M., 2019. New directions in studying the evolution of play. In: Smith, P.K., Roopnarine, L. J. (Eds.), The Cambridge Handbook of Play: Developmental and Disciplinary Perspectives. Cambridge University Press, pp. 11–29.

Burghardt, G.M., Ward, B., Rosscoe, R., 1996. Problem of reptile play: environmental enrichment and play behavior in a captive Nile soft-shelled turtle, *Trionyx triunguis*. Zoo. Biol. 15, 223–238. https://doi.org/10.1002/(SICI)1098-2361(1996)15:3%3C223::AID-ZOO3%3E3.0.CO;2-D.

Burghardt, G.M., Chiszar, D., Murphy, J., Romano, J., Walsh, T., Manrod, J., 2002. Behavioral diversity, complexity, and play in Komodo dragons. In: Murphy, J., Ciofi, J., de La Panouse, C., Walsh, T. (Eds.), The Biology and Conservation of Komodo Dragons. Smithsonian Press, pp. 78–117.

Burghardt, G.M., Dinets, V., Murphy, J.B., 2015. Highly repetitive object play in a cichlid fish (*Tropheus duboisi*). Ethology 121, 38–44. https://doi.org/10.1111/eth.12312 https://doi.org/10.1017/9781108131384.

Caro, T.M., 1988. Adaptive significance of play: Are we getting closer? Trends Ecol. Evol. 3, 50–54.

Colbert, E.H., Morales, M., Minkoff, E.C., 2001. Colbert's Evolution of the Vertebrates: a History of the Backboned Animals Through Time, 5th edition. Wiley-Liss.

Cooper, M.A., Grizzell, J.A., Whitten, C.J., Burghardt, G.M., 2023. Comparing the ontogeny, neurobiology, and function of social play in hamsters and rats. Neurosci. Biobehav. Rev. 147, 105102 https://doi.org/10.1016/j.neubiorev.2023.105102.

Cooper, W.E., 1971. Display behavior of hatchling *Anolis carolinensis*. Herpetologica 27, 498–500. ⟨http://www.jstor.org/stable/3891292⟩.

Dapporto, L., Turillazzi, S., Palagi, E., 2006. Dominance interactions in young adult paper wasp (*Polistes dominulus*) foundresses: A playlike behavior? J. Comp. Psychol. 120, 394–400 https://psycnet.apa.org/doi/10.1037/0735-7036.120.4.394.

Darwin, C., 1845. Voyages of the Beagle Round the World. Murray.

Dinets, V., 2011. *Crocodylus rhombifer* (Cuban crocodile) courtship behavior. Herpetol. Rev. 42, 232.

Dinets, V., 2015. Play behavior in crocodilians. Anim. Beh. Cogn. 2, 49–55. https://doi.org/10.12966/abc.02.04.2015.

Dobson, D., 2010. Why fish jump. Available online: ⟨https://www.landbigfish.com/articles/default.cfm?ID=566⟩.

Doody, J.S., Burghardt, G.M., Dinets, V., 2013. Breaking the social–non-social dichotomy: a role for reptiles in vertebrate social behavior research? Ethology 119, 95–103. https://doi.org/10.1111/eth.12047.

Doody, J.S., Dinets, V., Burghardt, G.M., 2021. JHU Press. Secret Soc. Lives Reptiles.

Eisenbeiser, S., Serbe-Kamp, É., Gage, G.J., Marzullo, T.C., 2022. Gills just want to have fun: can fish play games, just like us? Animals 12, 1684. https://doi.org/10.3390/ani12131684.

Fagen, R.M., 1981. Animal Play Behavior. Oxford University Press,.

Fagen, R.M., 2017. Salmonid jumping and playing: Potential cultural and welfare implications. Animals 7, 42. https://doi.org/10.3390/ani7060042.

Fishbase, 2023. ⟨https://fishbase.org⟩. Accessed 23 April 2023.

Gallup, G.G.Jr, Anderson, J.R., 2018. The "olfactory mirror" and other recent attempts to demonstrate self-recognition in non-primate species. Behav. Process. 148, 16–19. https://doi.org/10.1016/j.beproc.2017.12.010.

Gilbert, P.W., 1967. Sharks, Skates and Rays. John Hopkins University Press,.

Greenberg, N., Hake, L., 1990. Hatching and neonatal behavior of the lizard, *Anolis carolinensis*. J. Herpetol. 24, 402–405. https://doi.org/10.2307/1565058.

Grigg, G., Kirshner, D., 2015. Comstock Publishing Associates. Biol. Evol. Crocodylians.

Grigg, G., Nowack, J., Bicudo, J.E.P.W., Bal, N.C., Woodward, H.N., Seymour, R.S., 2022. Whole-body endothermy: ancient, homologous and widespread among the ancestors of mammals, birds and crocodylians. Biol. Rev. 97, 766–801. https://doi.org/10.1111/brv.12822.

Gudger, E.W., 1944. Fishes that play "leapfrog. Am. Nat. 78, 451–463. https://doi.org/10.1086/281216.

Halpern, M., Frumin, N., 1979. Roles of the vomeronasal and olfactory systems in prey attack and feeding in adult garter snakes. Physiol. Behav. 22, 1183–1189.

Heinbuch, B., Wiegman, T., 2000. Unusual behavior of dwarf caiman. Crocodile Spec. Group Newsl. 19, 14–15.

Hill, C., 1946. Playtime at the zoo. Zoo. Life 1, 24–26.

Holder, C.F., 1892. Appleton. Fla. Reef.

Howard, D., Freeman, M.S., 2022. Overlooked and under-studied: A review of evidence-based enrichment in Varanidae. J. Zool. Bot. Gard. 3, 32–43. https://doi.org/10.3390/jzbg3010003.

Huizinga, J., 1938. Homo Ludens: A Study of the Play Element in Culture. Routledge,.

Hurme, K., Gonzalez, K., Halvorsen, M., Foster, B., Moore, D., Chepko-Sade, B.D., 2003. Environmental enrichment for dendrobatid frogs. J. Appl. Anim. Welf. Sci. 6, 285–299. https://doi.org/10.1207/s15327604jaws0604_3.

Iwaniuk, A.N., Nelson, J.E., Pellis, S.M., 2001. Do big-brained ace analyses of play and relative brain size in mammals. J. Compar. Psychol. 115, 29.

Jarmer, K., 1928. Das Seelenleben der Fische. R. Oldenbourg,.

Kane, D., Davis, A.C., Michaels, C.J., 2019. Play behaviour by captive tree monitors, *Varanus macraei* and *Varanus prasinus*. Herpetol. Bull. 149, 28–31. https://doi.org/10.33256/hb149.2831.

Kaplan, G., 2020. Play behaviour, not tool using, relates to brain mass in a sample of birds. Sci. Rep. 10 (1), 15. https://doi.org/10.1038/s41598-020-76572-7.

Khandakar, N., Jeny, K.N., Islam, S., Hakim, M.A., Pony, I.A., 2020. Play behavior by a yellow monitor, *Varanus flavescens* (Hardwicke and Gray 1827). Rept. Amphib. 27, 257–258.

Khokhlenko, D.M., 1959. Разведение стерляди [Sterlet Breeding]. Ukrselkhozizdat [in Russian].

Klausewitz, W., 1966. Ein bemerkenswerter Zähmungsversuch an freilebenden Fischen. Natür und Volk 90, 91–96.

Kotrschal, K., 2000. Taste (s) and olfaction (s) in fish: a review of spezialized sub-systems and central integration. Pflüg. Arch. 439, r178–r180. https://doi.org/10.1007/s004240000137.

Kramer, M., Burghardt, G.M., 1998. Precocious courtship and play in emydid turtles. Ethology 104, 38–56. https://doi.org/10.1111/j.1439-0310.1998.tb00028.x.

Krause, M.A., Burghardt, G.M., Lentini, A., 1999. Object provisioning for Nile soft-shelled turtles (*Trionyx triunguis*). Lab Anim. 28, 38–41.

Kuba, M.J., Byrne, R.A., Burghardt, G.M., 2010. A new method for studying problem solving and tool use in stingrays (*Potamotrygon castexi*). Anim. Cogn. 13, 507–513. https://doi.org/10.1007/s10071-009-0301-5.

Kuba, M.J., Gutnick, T., Burghardt, G.M., 2014. Learning from play in octopus. In: Darmaillacq, A.-S., Dickel, L., Mather, J. (Eds.), Cephalopod Cognition. Cambridge University Press, pp. 57–67.

Ladiges, W., 1954. Der Sterlet in Aquarium. Die Aquar. - und Terr. Z. 7, 200–202.

Lazell, J.D.Jr, Spitzer, N.C., 1977. Apparent play behavior in an American alligator. Copeia (1), 188.

Lepage, D. (editor), 2023. Avibase, ⟨https://avibase.bsc-eoc.org/⟩, accessed 23 April 2023.

Mammal Diversity Database, 2023. Mammal Diversity Database (Version 1.11) [Data set]. Zenodo. https://doi.org/10.5281/zenodo.4139818.

Mann, M.A., Mellgren, R.I., 1998. Sea turtle interactions with inanimate objects: autogrooming or play behavior? In: Byles, R., Fernandez, Y. (Eds.), Proceedings of the Sixteenth Annual Workshop on Sea Turtle Biology and Conservation, pp. 93–94. Washington, D.C.: NOAA Technical Memorandum NMFS-SEFSC-412.

Manrod, J.D.W., 2003. Object introduction, exploration, and play behavior in black-throated monitor lizards (*Varanus albigularis albigularis*). M.Sc. thesis, University of Tennessee, available at ⟨https://trace.tennessee.edu/utk_gradthes/5259/⟩.

Meder, E., 1958. *Gnathonemus petersii* (Günther). Z. für Vivari-.-. 4, 161–171.

Meyer-Holzapfel, M., 1960. Über das Spiel bei Fischen, insbesondere beim Tapirrüsselfisch (*Mormyrus kannume* Forskål). Zool. Gart. 25, 189–202.

Mo, M., 2020. Only in captivity?: An interaction between two threatened chelonians, an Asian giant tortoise (*Manouria emys*) and a Malaysian giant turtle (*Orlitia borneensis*). Rept. Amphib. 27, 89–90. https://doi.org/10.17161/randa.v27i1.14470.

Nielsen, J.L., 1990. Environment and behavior affecting growth and development of juvenile coho salmon (*Oncorhynchus kisutch*) (M.S. thesis). University of California, Berkeley.

Nunes, S., Montemayor, M.P.M., 2023. Multiple benefits of juvenile play: a ground squirrel's perspective. Neurosci. Biobehav. Rev. . 145, 105099 https://doi.org/10.1016/j.neubiorev.2023.105099.

Pellis, S., Pellis, V., 2009. The playful brain: venturing to the limits of neuroscience. Oneworld.

Pellis, S.M., 1981. Exploration and play in the behavioural development of the Australian magpie *Gymnorhina tibicen*. Bird. Behav. 3, 37–49. https://doi.org/10.3727/015613881791560900.

Pellis, S.M., Pellis, V.C., 2021. Play (In: Braddick, O. (Ed). Oxford Research Encyclopedia of Psychology. Oxford University Press,. https://doi.org/10.1093/acrefore/9780190236557.013.791.

Pellis, S.M., Pellis, V.C., Ham, J.R., Stark, R.A., 2023. Play fighting and the development of the social brain: The rat's tale. Neurosci. Biobehav. Rev. 145, 105037 https://doi.org/10.1016/j.neubiorev.2023.105037.

Proctor, J.B., 1928. On a living Komodo Dragon *Varanus komodoensis* Ouwens, exhibited at the Scientific Meeting, October 23, 1928. Proc. Zool. Soc. Lond. 98, 1017–1019. https://doi.org/10.1111/j.1469-7998.1928.tb07181.x.

Pruitt, J.N., Burghardt, G.M., Riechert, S.E., 2012. Non-conceptive sexual behavior in spiders: a form of play associated with body condition, personality type, and male intrasexual selection. Ethology 118, 33–40. https://doi.org/10.1111/j.1439-0310.2011.01980.x.

Rivas, J., Burghardt, G.M., 2002. Crotalomorphism: A metaphor for understanding anthropomorphism by omission. In: Bekoff, M., Allen, C., Burghardt, G.M. (Eds.), The cognitive animal: Empirical and theoretical perspectives on animal cognition. MIT Press, pp. 9–18.

Rothschild, B.M., 2015. Unexpected behavior in the Cretaceous: tooth-marked bones attributable to tyrannosaur play. Ethol. Ecol. Evol. 27, 325–334. https://doi.org/10.1080/03949370.2014.928655.

Rowland, H.M., Rockwell Parker, M., Jiang, P., Reed, D.R., Beauchamp, G.K., 2015. Comparative taste biology with special focus on birds and reptiles. Handbook of Olfaction and Gustation, 3rd edition.,. John Wiley & Sons, Inc,, pp. 957–982.

Schoch, R.R., Sues, H.D., 2015. A Middle Triassic stem-turtle and the evolution of the turtle body plan. Nature 523, 584–587. https://doi.org/10.1038/nature14472.

Schwing, R., Wein, A., 2016. Object pay in a teiid lizard. Poster at the 8th European Conference on Behavioural Biology, Vienna, Austria, 12–15 July 2016, image available at 〈https://www.facebook.com/groups/336872486468373/posts/645518168937135/〉.

Shackley, M., 1998. 'Stingray City'-managing the impact of underwater tourism in the Cayman Islands. J. Sustain. Tour. 6, 328–338. https://doi.org/10.1080/09669589808667320.

Siegel, M.A., Jensen, R.A., 1986. The effects of naloxone and cage size on social play and activity in isolated young rats. Behav. Neural Biol. 45, 155–168. https://doi.org/10.1016/S0163-1047(86)90739-9.

Smaldino, P.E., Palagi, E., Burghardt, G.M., Pellis, S.M., 2019. The evolution of two types of play. Behav. Ecol. 30, 1388–1397. https://doi.org/10.1093/beheco/arz090.

Soares, D., Bierman, H.S., 2013. Aerial jumping in the Trinidadian guppy (*Poecilia reticulata*). PLoS ONE 8 (4), 10. https://doi.org/10.1371/journal.pone.0061617.

Stell, E., 2018. Leaping behavior in silver carp (Hypophthalmichthys molitrix): analysis of burst swimming speeds, angle of escape, height, and distance of leaps. M. Sc. thesis, University of Mississippi, available at 〈https://egrove.olemiss.edu/etd/374/〉.

Sulak, K., Edwards, R.E., Hill, G.W., Randall, M., 2002. Why do sturgeons jump? Insights from acoustic investigations of the Gulf sturgeon in the Suwannee River, Florida, USA. J. Appl. Icthyol. 18, 617–620. https://doi.org/10.1046/j.1439-0426.2002.00401.x.

Thonhauser, K.E., Gutnick, T., Byrne, R.A., Kral, K., Burghardt, G.M., Kuba, M.J., 2013. Social learning in Cartilaginous fish (stingrays *Potamotrygon falkneri*). Anim. Cogn. 16, 927–932. https://doi.org/10.1007/s10071-013-0625-z.

Uetz, P.. (editor), 2022. The Reptile Database, 〈http://www.reptile-database.org/〉, accessed 23 April 2023.

Wegner, N.C., Snodgrass, O.E., Dewar, H., Hyde, J.R., 2015. Whole-body endothermy in a mesopelagic fish, the opah, *Lampris guttatus*. Science 348, 786–789 https://www.science.org/doi/abs/10.1126/science.aaa8902.

Williams, G.C., 1991. Natural Selection. Oxford University Press,.

Zeiträg, C., Jensen, T.R., Osvath, M., 2023. Play in juvenile greater rheas: different modes and their evolutionary and socio-cognitive implications. Intern. J. Play 16 (1). https://doi.org/10.1080/21594937.2022.2152532.

Zhang, H., Peng, Y., Li, C., Lan, H., Xing, G., Chen, Z., Zhang, B., 2020. Playing mahjong for 12 weeks improved executive function in elderly people with mild cognitive impairment: A study of implications for TBI-induced cognitive deficits. Front. Neurol. 11, 178 https://doi.org/10.3389/fneur.2020.00178.