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Review

The Herbicide Glyphosate and Its Formulations Impact Animal Behavior across Taxa

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Abstract: Use of glyphosate and glyphosate-based herbicides is ubiquitous in US agriculture and widespread around the world. Despite marketing efforts to the contrary, numerous studies demonstrate glyphosate toxicity to non-target organisms including animals, primarily focusing on mortality, carcinogenicity, renal toxicity, reproductive, and neurological toxicity, and the biochemical mechanisms underlying these physiological outcomes. Glyphosate toxicity also impacts animal behavior, both in model systems and in agricultural and environmentally relevant contexts. In this review, we examine the effects of glyphosate and glyphosate-based herbicides on animal behaviors, particularly activity, foraging and feeding, anti-predator behavior, reproductive behaviors, learning and memory, and social behaviors. Glyphosate can be detected both in food and in the environment, and avoided through activity and feeding strategies. However, exposure also reduces activity, depresses foraging and feeding, increases susceptibility to predation, interferes with courtship, mating, fertility and maternal behaviors, decreases learning and memory capabilities, and disrupts social behaviors. Changes in animal behavior as a result of glyphosate toxicity are important because of their sometimes severe effects on individual fitness, as well as ecosystem health. Implications for human behavior are also considered.

Keywords: glyphosate; Roundup®; activity; feeding; anti-predator; reproductive behavior; maternal behavior; learning; memory; social behavior

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1. Introduction

Glyphosate-based herbicides (GBHs), including brands such as Roundup®, are the most used pesticides in the United States and for the world as a whole [1]. Commercial farmers spray GBHs in three main application contexts: (1) as a pre-planting herbicide, reducing competition for seedlings and young plants; (2) to reduce competition throughout the growing season on Roundup® Ready crops, including most of the corn, sugar beets, soy, and canola, and smaller portions of zucchini, alfalfa, and other crops, grown in the US; and (3) to kill leafy vegetation before harvest and ease separation of non-vegetative, commercially important parts of crop plants, used extensively for sugar cane, wheat, oats, and legumes. Perhaps because of the timing of application, this last type of use seems to impact food supplies most greatly, since glyphosate residue concentrations measured in oat- and wheat-based foods are the highest among all the foods tested [2,3]. Yet these crops are not genetically modified to be herbicide-tolerant; though herbicide tolerant soybeans also contain high concentrations of glyphosate residue [4]. This results in continuous, low-concentration human exposure to residues through food [5] and, because of runoff, drift, and overspray, in drinking water and the environment for both humans and other animals that live in or near agricultural areas. In addition, GBHs are used extensively by homeowners to suppress vegetation around driveways, walkways and fence lines, and by public employees to suppress weeds in public spaces like sidewalks, parking lots, playgrounds, and schools. Therefore, during application and subsequent exposure, humans and other animals living in urban, suburban and rural environments can all be exposed sporadically to higher doses of GBHs (e.g., [6]; Table 1). This supposition is borne out by examining glyphosate concentration in tissues (personal observation; [7–10]), including its prevalence in human urine (reviewed in [11]), related to type of exposure (occupational vs. dietary; [12]) and type of diet (organic vs. conventional; [13]).

Table 1. Selected types of GBH exposure from application, national standards, water, and food; and the range of concentrations at which they occur.

Exposure Type	Concentration	Source
Homeowner-grade Roundup® application recommended concentration	2% or 20 g glyphosate/L herbicide	MSDS, Roundup Ready to Use®
Agricultural-grade Roundup® application recommended concentration	up to 6.2% or 62 g glyphosate/L herbicide; or 20.5 oz glyphosate/acre	Roundup Powermax 3® label
US: acceptable daily intake	1.75 mg/kg/day	[14]
EU: acceptable daily intake	0.5 mg/kg/day	[15]
EU: acceptable operator exposure level	0.1 mg/kg/day	[15]
Australia: acceptable daily intake	0.3 mg/kg/day	[14]
Canada: safe for aquatic life	800 μg/L	[16]
Agricultural topsoils, Europe	up to 2.05 mg/kg glyphosate up to 1.95 mg/kg AMPA, its major metabolite	[17]
Surface water	34–430 μg/L	[18]
Surface water runoff	up to 5200 μg/L	[19]
Oversprayed wetlands	0.33 +/− 0.11 mg/L	[20]
Groundwater, Hopelchén, Campeche, Mexico	0.44–1.41 μg/L	[21]
Companion animal feeds (dog and cat food)	78.3–2140 μg/kg	[22]
Bee bread	0–700 ng/g	[23]
Honey	up to 163 μg/kg	[14]
Honey, Kaua‘i Hawaii	average 118.3 μg/L	[14]
Beer, Germany	0.46–29.74 μg/L	[14]
Beer, California	9.1–49.7 μg/L	[14]
Wine, California	36.3–51.4 μg/L	[14]
Soybeans, genetically modified	9 mg/kg	[4]
Soybean grains (US; USDA)	0.265–18.53 mg/kg	[14]
Soybean grains (US; FDA)	0.003–10 mg/kg	[14]
Soy sauce	up to 564 μg/L	[14]
Chick peas	up to 11 mg/kg	[24]
Great Value chickpeas	889 ppb	[2]
Lentils	up to 9 mg/kg	[24]
Lentils, Europe	0.01–11 mg/kg	[14]
Lentils, HyVee	535 ppb	[2]
Green split peas, Good & Gather	168 ppb	[2]
Buckwheat, Europe	0.02–12.7 mg/kg	[14]
Barley, Europe	0.02–8.9 mg/kg	[14]
Barley	up to 1.7 mg/kg	[24]
Corn (FDA)	0.002–4.5 mg/kg	[14]
Wheat, Europe	0.01–2.9 mg/kg	[14]
Wheat kernels	up to 1.1 mg/kg	[24]
Rye, Europe	0.01–1.8 mg/kg	[14]
Oat, Europe	0.68–0.82 mg/kg	[14]
100% whole wheat bread, Village Hearth	1150 ppb	[2]
Oats, Quaker	535 ppb	[2]
Cheerios	1125.3 ppb glyphosate 26.4 ppb AMPA	[2]
Pita Chips, Stacy’s Simply Naked by Frito-Lay, Pepsi-Co	812.5 ppb	[2]
Crackers, Ritz	270.2 ppb	[2]
Plant-based protein bar, chocolate, Onnit	134 ppb	[2]

The marketing of Roundup® focuses on its safety for animals based on two incorrect assumptions. Several different formulations are sold commercially, different formulations are sold in different countries, and those available to the public are slightly different from the formulations marketed for agriculture. To date, the active ingredient of all formulations is glyphosate, though secondary herbicides may also be included. The first argument for the safety of Roundup® for animals is that glyphosate targets the shikimate pathway of amino acid synthesis, which is present in plants and microbes, but not in animals. Of course this does not preclude the possibility that glyphosate also interacts with other molecules to create toxic secondary effects. The second argument depends on experimental results showing that, when tested alone by Roundup® manufacturers or scientists funded by them, glyphosate exhibited low toxicity to mammals. Regulatory agencies have never required testing of so-called inert ingredients within the various formulations, and tests with the whole GBH formulations are not required to get approval for marketing. Other ingredients within the various formulations, particularly the secondary herbicides and surfactants, have proven either to act synergistically, increasing the toxicity of glyphosate, or to be more toxic than glyphosate, e.g., [25–28]. These effects are difficult to explore fully because the composition of each formulation is considered proprietary and therefore, herbicide manufacturers do not have to disclose the ingredients; and the composition of formulations can differ from country to country. Given the wide variety of animal species and biological systems known to be disrupted by GBH exposure, one or both of these arguments must be incorrect.

Thousands of peer-reviewed articles have been published that demonstrate toxic effects of glyphosate and/or GBH formulations on animals (Table 2). A thorough review of all the toxic effects reported across all animal taxa studied is beyond the scope of any single review article, but particular types of GBH toxicity have been reviewed. Some particularly thorough reviews discuss health risks [29–32] and ecotoxicology [33], while more focused reviews elaborate on the effects on water fleas [34], on bees [35] and honeybees [36,37], on fish [38], on amphibians [39], in South American agriculture [40], as studied in Brazil [41], in aquatic systems [42,43], and to offspring of exposed mothers [44]. Other reviews focus on particular outcomes of toxicity, including cancer and genotoxicity [45–47], pregnancy outcomes [48–50], mammalian nervous systems [51], and autism spectrum disorders [52–55]. Since it is apparent that the effects of glyphosate and of GBH formulations often differ (reviewed in [28,56]), this distinction must be considered when possible.

Table 2. Acute mortality induced by glyphosate or GBH from selected studies. Lower LD_{50}/EC_{50} indicates higher sensitivity to exposure.

Toxicity Measure	LD_{50}/EC_{50}	Source
Acute oral toxicity, Rat	5000 mg/kg (no deaths)	MSDS for Roundup Powermax 3®
Wistar rats, 60 ± 10 days old, 24–28 h exposure, acute oral toxicity	males 7203.58–7397.25 mg/kg females 7444.26–7878.50 mg/kg	[57]
Acute inhalation toxicity, Rat	2.23 mg/L	MSDS for Roundup Powermax 3®
Acute dermal toxicity, Rat	5000 mg/kg (no deaths)	MSDS for Roundup Powermax 3®
Anurans, *Rana catesbeiana* and *R. clamitans*, larval (Gosner stage 25), 96 h static renewal and non-renewal exposure	0.8–4.6 mg/L	[42]
Anurans, larval, North America, 96 h static, nonrenewed aqueous exposure	1.80–4.22 mg/L	[58]
Onchorynchus mykiss, 96 h	swim ups 1.8 mg/L adults 6.1 mg/L	[42]
Pimephales promelas, adult, 24 h static aqueous exposure	1.7 mg/L	[42,59]
Eisenia fetida, acute (14 days)	glyphosate acid 5600 mg/kg dry soil MON 52276 > 388 mg/kg dry soil	[15]
Apis mellifera (methodology not specified)	10 mg/L	[60]
Drosophila melanogaster, depending on formulation and sex	48 h 6.02–199 g/L 7 days 2.67–8.97 g/L	[61]
Acartia tonsa (crustacean), 48 h exposure	1.77 mg/L	[42,43]
Marine crustaceans, depending on species, temperature and formulation, 48 or 96 h exposure	6.57 to >500 mg/L	[62]
Artemia salina (microcrustacean), early life stage, 48 h exposure in artificial seawater	Roundup Original® 14.19 mg/L Glyphosate AKB 480 37.53 mg/L	[33]
Aquatic algae, 72 or 96 h exposure	3.5–55.9 mg/L	[42]

Agricultural workers and others living in agricultural areas likely experience particularly high GBH exposure, e.g., [6,12,63]. While it is extremely difficult to study in detail, in human agricultural workers, herbicide exposure is implicated in cases of impaired kidney function [64], altered thyroid and reproductive hormone levels [65], and reduced sperm count [66,67], and increases time to pregnancy [68], chance of short gestation [69], preterm birth [70], and neurobehavioral birth defects in their children [71], perhaps partially by increasing the permeability of the blood–brain barrier and changing the metabolic activity of epithelial cells in the brain [72]. Workers in GBH factories experience increased likelihood of coronary artery disease [73]. Probability of advanced liver fibrosis in patients with fatty liver disease [74] is associated with GBH exposure, as are Parkinson's Disease and parkinsonism [75–77], and autism spectrum disorders [78,79]. Experimentally, GBH exposure decreases human sperm motility [80]; transiently increases genotoxicity [81] via DNA lesions [82] and increases formation of micronuclei in peripheral white blood cells [83]; mimics estradiol in inducing the growth of cholangiocarcinoma cells [84]; induces genomic damage on human lymphocytes [85]; induces breast cancer cell growth through an estrogen receptor pathway [86]; and, at low doses, dysregulates gene expression in breast cancer cell lines, particularly in pathways related to cell cycle and DNA damage repair [87]. Consistent with cancer cell line studies, the development of non-Hodgkin lymphoma [47,88,89] and other cancers [90] have been correlated with GBH exposure. Human suicide attempts using GBH impair cardiac function [91], require attention to airways and cause renal damage [92], and may induce gastrointestinal symptoms and central nervous system complications [93,94] including hippocampal infarction [95].

Following the suggestion of Clotfelter et al. [96] and Zala and Penn [97], who point out the importance of exploring the role of animal behavior when studying toxic chemical pollutants and endocrine disruptors, this review explores the toxic effects of GBHs on the behavior of animals. Based on the research articles available, we focus on the toxic effects of glyphosate and glyphosate-based herbicides across animal taxa on activity level, feeding behavior, anti-predator behavior, reproductive and maternal behavior, learning and memory, and anxiety-like and social behavior.

2. Materials and Methods

The research reviewed in this article was collected in two ways. First, we conducted exhaustive searches using Google Scholar, Science Direct, and Wiley Online Library, using Biological Abstracts and GreenFile for verification in a few searches wherein all articles were identified with the initial three databases. Likewise, we combined each behavior-related search term with “glyphosate”, and for some of these, separately searched “Roundup®” to verify that the same relevant articles were identified. Each of these databases was searched between October 2022 and March 2023 using the search terms listed in Table 3, with the number of hits indicated. From each search, we identified articles based on their title that were about how glyphosate or glyphosate-based herbicides like Roundup® affect behavior. If the title was not sufficient to determine whether each paper focused on an appropriate topic, the abstract was read as well. For each search, once we encountered between five and ten articles in a row that were not relevant to our topic, we stopped reading titles from that search. Only peer-reviewed research articles were included, not review articles, abstracts, conference proceedings, or theses. The resulting set of articles was then sorted into these behavioral categories: activity, feeding behavior, anti-predatory behavior, reproductive and maternal behavior, learning and memory, and anxiety and social behavior.

Table 3. Number of matches from each search term in each database. The first number is the number of “hits” using each set of search terms, the second is the number the authors examined and assessed for appropriateness, and the third is the number of articles included in the review that were identified via that search. These do not add up to the total number of articles used because of extensive overlap between searches.

	Google Scholar	Science Direct	Wiley Online Library
Glyphosate behavior	51,100/130/20	5613/100/11	2752/80/1
Roundup® behavior	58,800/130/7	1780/125/5	1968/20/0
Glyphosate anti-predator behavior	328/110/14	168/29/12	101/2/0
Roundup® anti-predator behavior	373/90/16	67/19/9	93/20/0
Glyphosate feeding behavior	23,000/140/17	2119/142/7	1379/54/5
Glyphosate sexual behavior	13,600/80/13	530/50/13	612/60/1
Glyphosate courtship	593/80/7	37/37/2	18/18/0
Glyphosate mating behavior	5540/80/10	658/50/2	428/60/1
Glyphosate maternal behavior	4930/70/10	446/50/5	257/60/3
Glyphosate animal activity	47,700/90/4	5637/150/5	3529/40/0
Roundup® animal activity	40,900/70/2	1762/75/2	1629/40/0
Glyphosate learning behavior	18,500/60/32	545/50/11	512/20/5
Glyphosate memory	9360/60/28	607/50/10	343/20/3
Glyphosate anxiety	5900/60/28	326/50/13	167/20/7

The second method we used to identify articles to include in this review was using the bibliographies of the articles identified using the first method, particularly the review articles cited in the introduction. These were sorted into the same behavioral categories.

Some articles included experiments relevant to more than one category, and these were included in both or all, and the resulting number of articles in each behavioral category are distributed by taxa in Table 4. The 128 articles included in our results are distributed by taxa as shown in Figure 1. Each behavioral category was then assigned to one of the authors, who read the articles, compiled the information, and wrote the first draft of the relevant section. Frequent discussions among the authors identified focal topics within and among behavioral categories and key themes for discussion, and every author commented on each section.

Table 4. Number of research articles used for each section of this review by taxa.

Taxa	Activity	Feeding	Predator Avoidance	Reproductive Behavior	Learning and Memory	Social Behaviors
Bees	9	7	0	0	8	4
Aquatic invertebrates	0	3	2	0	0	0
Other terrestrial invertebrates	14	9	3	11	1	0
Fish	16	2	6	7	2	5
Amphibians and Reptiles	3	1	5	0	1	0
Birds	0	1	0	0	0	0
Rodents	5	0	0	9	5	15
Humans	0	0	0	0	6	5
Total	38	23	14	27	23	29

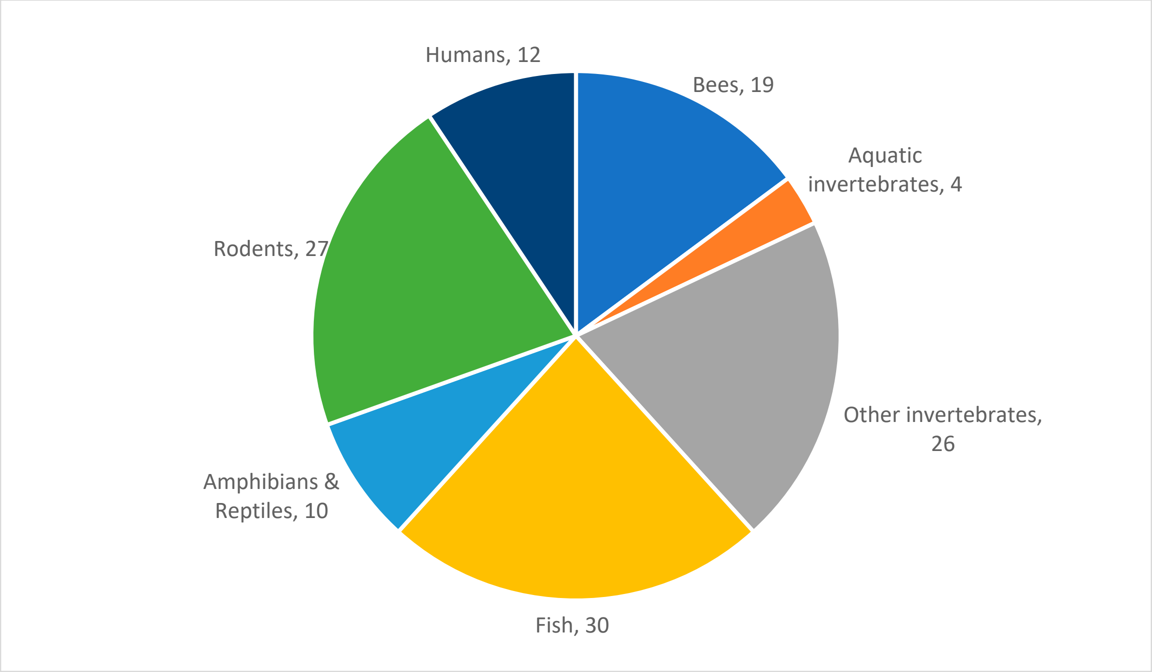

Figure 1. Number of papers by taxa. This indicates the animal group studied and the number of papers about that group for all research articles which met inclusion criteria and are cited herein.

3. Results

3.1. Activity

Glyphosate affects the way many animals go about their day to day lives. Across studies about animal activity in a wide range of taxa, glyphosate affects activity levels, whether walking, crawling, swimming, or flying. When exposed to glyphosate, animals tend to be less active and do not move as far as unexposed animals (summarized in Table 5). In the honeybee, *Apis mellifera*, an experiment conducted using 7 µg glyphosate/bee, 14 µg/bee, and 28 µg/bee found that exposure to higher concentrations caused the bees to have trouble reaching their hive [98]. Bees returning to the hive in a straight line or with five right-angle turns, 2 h after being fed sucrose solution containing 5 mg/L or 10 mg/L glyphosate, took more time to reach the hive in both sets of mazes [60]. A similar method was used by Balbuena et al. [99] to examine flight paths of bees after food-based glyphosate exposure at 2.5 mg/L, 5 mg/L, or 10 mg/L. Although they performed this study outside and not under laboratory conditions, bees given herbicide took longer and took fewer direct flights. Similarly, 2.5 mg/L glyphosate exposure strongly impacted how long it took bees to return home [36]. A different method was used to record total activity level over a 24 h period. Bees were more active than controls when exposed to Roundup® at 1.2 mg/L or 6 mg/L, whereas exposure at 0.12 mg/L and 12 mg/L did not affect their activity levels, and exposure to 24 mg/L of Roundup® decreased their activity [100]. While this is an unusual response pattern, the mechanism leading to this change in behavior is not known. If the change in activity results from the endocrine-disruptive properties of GBHs, which are known to be non-monotonic, this may not be surprising (e.g., [101]). Conversely, feeding 50- or 100-ng doses of glyphosate per bee, caused bees to sleep more [102]. Other studies did not identify changes in activity level after Roundup® or glyphosate exposure. At concentrations of 0.5 mL/50 mL, 1 mL/50 mL, and 1.5 mL/50 mL, bees successfully returned to the hive [103]. However, these authors only considered whether the bees returned to the hive and not activity level or speed of return. Another study tested locomotion using a square box with four lights. One light was turned on at a time and when the bee was at the light it would turn off and the next light would turn on. This is an effective way to collect activity data because bees go toward lights. The data collected then were the duration of time it took for the bees to get to all the lights twice. When conducting this experiment with bees exposed to glyphosate at a concentration of 2.5 mg/L or 5 mg/L, they did not find a significant difference among the groups [104].

Walking animals also exhibit lower activity levels after exposure to glyphosate. In Swiss mice, the total distance traveled and velocity decrease when exposed to higher concentrations of GBHs given in oral gavages [105,106]. Exposure of mice to 50 mg/kg/day of a GBH had a large effect on their activity. The mice were less active and traveled a shorter distance than unexposed controls [107]. The Sprague Dawley rat also exhibited less locomotor activity when first injected with glyphosate at concentrations of 50, 100, or 150 mg glyphosate/kg. The rats traveled shorter distances, had less activity, and showed less stereotyped behavior in a dose-dependent pattern [108]. Another study showed less locomotor activity of Wistar rats injected with glyphosate at the lower concentration of 35 mg glyphosate/kg [109].

Similarly, arthropods also showed lower locomotor activity after GBH exposure. Arthropods tested include the small wolf spider, *Pardosa milvina*; the large wolf spider, *Hogna helluo*; and the ground beetle, *Scarites quadriceps*. All three arthropods showed a decrease in activity when they came in contact by touch with the herbicide [110]. The Madagascar hissing cockroach, *Gromphadorhina portentosa*, consumed up to 13.2 mg of glyphosate. Then, they were placed on a hamster wheel to see how long they could run for a maximum of 3 min. The results showed a significant decrease in time spent running on the wheel for cockroaches exposed to glyphosate compared to their unexposed conspecifics [111]. The fruit fly, *Drosophila melanogaster*, was also studied to see how different methods of feeding could affect their locomotor activity. The methods they used were putting the pesticide into agar-gelled feed (AM) and continuous liquid feeding (CLF), where flies ingested the pesticide in liquid, and how much they ingested could be quantified. Both methods decreased locomotor activity, though CLF yielded lower locomotor levels than when using the AM method [112].

The earthworm, *Lumbricus terrestris*, is also impacted when exposed to glyphosate. The GBH induced lower levels of activity when present throughout the soil [113]. In another earthworm, *Octolasion cyaneum*, there was very slight avoidance behavior towards the contaminated soil at the concentration of 249 μg, though this slight avoidance was not statistically significant [114].

Many aquatic organisms, including several types of fish, decrease activity and behave abnormally when exposed to GBH. Many studies using the zebrafish, *Danio rerio*, show that GBHs lower activity level at all stages, from larvae to adult fish. In a study that used both larvae and adults, glyphosate and Roundup® at 0.01, 0.065, or 0.5 mg/L reduced swimming distance [115]. Glyphosate concentrations of 0.01, 0.5, or 5 mg/L also increased swimming activity levels in exposed larval and adult zebrafish during the day [116]. When exposed to glyphosate at 1000 μg/L, zebrafish larvae decreased swimming distance, number of rotations, mean velocity, and body mobility [117].

One study of larval zebrafish showed an increase in activity when exposed to GBH at the concentrations of 0.1 and 10 μM for a 7-day exposure period [118]. However, another study done on larval zebrafish showed an increase in activity levels when exposed to Roundup® at 10^6 to 10^4 dilution but a decrease when exposed to GBH at 0.01 and 0.1 μM. Both exposure periods were 48 h at 5 days after fertilization [119]. The common carp, *Cyprinus carpio*, showed a decrease in activity level when exposed for 60 days versus an increase in activity level when exposed for only 12 h to GBH [120,121]. Collectively, these results show that in zebrafish and carp, the effect of GBH on activity depends on both concentration and duration of exposure. One clue to the variation might be that when glyphosate circulates in the water in the tanks, carp moved away from the part of the tank with contaminated water [121]. Under some conditions, changes in activity might reflect avoidance of contaminated water, while under other conditions might reflect an impairment in ability to behave normally. For example, when exposed to higher concentrations of glyphosate, the African catfish, *Clarias gariepinus*, showed loss of reflex, air gulping, and erratic swimming [122]. Two other studies that exposed catfish to glyphosate documented loss of equilibrium, increased startle responses, abnormal swimming, and restlessness [123,124]. When treated with glyphosate, the redbelly tilapia, *Tilapia zilli*, swam erratically and irregularly. After bursts of swimming, they became exhausted, more so at higher concentrations [125]. An additional study using the livebearer, *Jenynsia multidentata*, showed lower swimming activity levels when exposed to GBH [126]. The blue ridge two-lined salamander, *Eurycea wildrae*, exhibited lower burst distance swimming activity when exposed to GBH, and lower movement distance at higher temperatures [127]. Conversely, in a study using the hybrid fish surubim, a cross-breed of *Pseudoplatystoma corruscans* and *Pseudoplatystoma reticulatum*, fish showed higher swimming activity levels and increased ventilatory frequency when exposed to GBH [128]. Furthermore, the rainbow trout, *Oncorhynchus mykiss*, was moved from dark to light and back to dark conditions while exposed to different concentrations and formulations of GBH, including glyphosate alone. During the light period, fish have significantly lower activity levels compared to the dark periods, though during the dark periods, the fish swam a longer distance [129].

Other aquatic animals affected by glyphosate include the marsh frog, *Pelophylax ridibundus*. Marsh frog tadpoles exposed to water contaminated with 7.6 mg/L, 3.1 mg/L, and 0.7 mg/L glyphosate showed a decrease in activity level during the Gosner stage 25 [130]. In two different species of South American frogs, *Boana faber* and *Leptodactylus latrans*, tadpoles showed lethargy, convulsions, and rapid bursts of swimming when exposed to glyphosate at concentrations of 69, 161, 310, 550, and 1074.5 μg/L [131]. However, in the leopard treefrog, *Boana pardalis*, there was an insignificant decrease in activity levels when frogs were exposed to glyphosate [132]. The water flea, *Daphnia magna*, showed less swimming activity when exposed to GBH [133].

Table 5. Effects of GBH on activity level.

Species	Herbicide/Ingredient Used	Exposure	Concentration	Results	Source
Honeybee (*A. mellifera*)	Herbazed 48%	Sucrose solutions	0.5 mL/50 mL 1 mL/50 mL 1.5 mL/50 mL	No effect on navigation	[103]
Honeybee (*A. mellifera*)	Glyphosate	Distilled water solutions containing glyphosate	2.5 mg/L 5 mg/L 10 mg/L	Longer to get to the hive	[99]
Honeybee (*A. mellifera*)	Glyphosate	Water and sucrose solutions containing glyphosate	1.2 mg/L 6 mg/L 0.12 mg/L 12 mg/L 24 mg/L	Decrease activity	[100]
Honeybee (*A. mellifera*)	Glyphosate	Sucrose solutions containing glyphosate	2.5 mg/L	Longer time to return to hive	[36]
Honeybee (*A. mellifera*)	Glyphosate	Water and sucrose solutions containing glyphosate	2.5 mg/L, 5 mg/L	No significant difference in activity	[104]
Honeybee (*A. mellifera*)	Glyphosate isopropylamine salt (Monsanto Roundup® Original)	Sucrose solutions containing herbicide	7 µg/bee, 14 µg/bee, 28 µg/bee.	Harder time reaching hive	[98]
Honeybee (*A. mellifera*)	Glyphosate	Sucrose solutions containing glyphosate	50, 100 ng doses	Cause bees to sleep more	[102]
Honeybee (*A. mellifera*)	Glyphosate, in the Roundup®	Sucrose solutions containing glyphosate	5 mg/L, 10 mg/L	Less time to reach the hive	[60]
Fruit fly (*D. melanogaster*)	Glyphosate	Continuous Liquid Feeding (CLF).	10 mM, 30 mM, 50 mM	Decreased locomotor activity	[112]
Swiss mice	Roundup®	Oral gavages	250 and 500 mg/kg/day	Total distance traveled and velocity decrease	[105,106]
CF-1 mice	Glyphosate isopropylamine salt	Saline solutions with glyphosate	50 mg/kg/day	Less active and traveled a shorter distance	[107]
Wistar rat	Glyphosate	Water solutions containing glyphosate	24 and 35 mg glyphosate/kg	Less locomotor activity	[109]
Sprague Dawley rat	Glyphosate	Saline solutions with glyphosate	50, 100, or 150 mg glyphosate/kg	Lower locomotor activity	[108]
Wolf spider (*P. milvina*; *H. helluo*) Ground beetle (*S. quadriceps*)	Glyphosate	Saline solutions with glyphosate	12 g/L	Lower locomotor activity	[110]
Madagascar hissing cockroach (*G. portentosa*)	Roundup® Ready-to-Use III	Food consumption	13.2 mg of glyphosate	Decrease in activity level	[111]
Earthworm (*O. cyaneum*)	Glyphosate	Distilled water solutions containing glyphosate	166, 332, 498, 664 and 830 g GLY/kg	Very slight avoidance of soil that contained glyphosate	[114]
Earthworm (*L. terrestris*)	Glyphosate based Herbicide	Food consumption	243, 221, 218 mg	Lower levels of activity	[113]
Salamander (*E. wildrae*)	Commercially sold Roundup®.	In water	0.0 mL/L, 0.5 mL/L, 1.0 mL/L, and 2.0 mL/L	Lower burst distance swimming activity and lower movement distance in higher temperatures	[127]
Rainbow trout larvae (*O. mykiss*)	Glyphosate based Herbicide	In water	1.18 ± 0.036 and 1.95 ± 0.086 µg/L	Increased swimming activity and distance traveled during dark periods	[129]
Redbelly tilapia (*T. zillii*)	Glyphosate based Herbicide	In water	108, 216, 324, 432 and 540 mg/L	Swam erratically and irregularly	[125]
Livebearer (*J. multidentata*)	Glyphosate based Herbicide	In water	0.59 ± 0.07, 0.58 ± 0.14 and 0.56 ± 0.16 mg/L	Lower swimming activity levels	[126]
Surubim(*P. corruscans* and *P. reticulatum* cross-breed)	Roundup® Original	In water	2.25, 4.5, 7.5, and 15 mg/L	Increase swimming activity levels and ventilatory frequency	[128]

Table 5. *Cont.*

Species	Herbicide/Ingredient Used	Exposure	Concentration	Results	Source
Carp (*C. carpio*)	Glyphosate	In water	5 and 15 mg/L	Decreased activity levels	[120]
Carp (*C. carpio*)	Glyphosate	In water	0, 50, 100 and 150 mL/L	Increased activity levels	[121]
African catfish (*C. gariepinus*)	Dizensate (Glyphosate Herbicide)	In water	9.6 mg/L, 14.4 mg/L, 19.2 mg/L, 21.6 mg/L and 24 mg/L	Loss of reflex, air gulping, and erratic swimming	[122]
African catfish (*C. gariepinus*)	Glyphosate	In water	0.36, 0.48, 0.60, 0.72 and 0.84 mg/L	Loss of equilibrium, increased startle responses, abnormal swimming, and restlessness	[123]
African catfish (*C. gariepinus*)	Glyphosate, in the Roundup®	In water	0.00 mg/L 0.30 mg/L 0.50 mg/L 0.70 mg/L 1.40 mg/L	Loss of equilibrium, increased startle responses, abnormal swimming, and restlessness	[124]
Zebrafish (*D. rerio*)	Glyphosate and Roundup®	In water	0.01 mg/L, 0.065 mg/L, and 0.5 mg/L	Reduced swimming distance at both stages	[115]
Zebrafish larvae (*D. rerio*)	Glyphosate	In water	0.05, 0.1, 0.5, 1, 10, 100, 1000, 10,000 mg/L	Decreased distance swam, number of rotations, mean velocity, and body mobility	[117]
Zebrafish larvae (*D. rerio*)	Glyphosate and Roundup®	In water	0.1, 1, and 10 μM GLY 10^6- to 10^4-fold dilution Roundup®	Increase activity levels with Roundup® exposure and decrease with glyphosate exposure	[119]
Zebrafish larvae (*D. rerio*)	Glyphosate	In water	0.01 and 10 μM	Increased in activity level	[118]
Zebrafish larvae (*D. rerio*)	Glyphosate	In water	0.01, 0.1, 0.5, 1, 5, and 10 mg/L	Increased swimming activity levels	[116]
Marsh frog tadpoles (*P. ridibundus*)	Roundup® Power 2.0	In water	7.6 mg/L, 3.1 mg/L, and 0.7 mg/L	Decrease in activity level at Gosner stage 25	[130]
Water flea (*D. magna*)	Glyphosate	In water	0, 0.875, 1.75, 3.5, 7, 14, 28, and 56 mg/L);	Lower swimming activity levels	[133]
Treefrog larvae (*B. pardalis*)	Glyphosate based Herbicides	Food exposure	2.40 mg/L, 4.00 mg/L, 1.21 mg/L,1.92 mg/L, 3.34 mg/L	Only ametryn had adverse side effects on the tadpole's activity	[132]
South American frog tadpoles (*B. faber* and *L. latrans*)	Glyphosate (Roundup Original DI®) + 2,4–D(NORTOX®)	In water	69, 161, 310, 550, and 1074.5 μg/L	lethargy, convulsions, and rapid bursts of swimming	[131]

3.2. Foraging and Feeding Behavior

Exposure to glyphosate-based herbicides alters the feeding behavior of some organisms, while in other studies it has no effect. In many cases, GBH-laden food is avoided (summarized in Table 6), while organisms pre-exposed to varying concentrations of GBHs for several hours or a few days before experimental trials only sometimes alter feeding behavior (summarized in Table 7). Zebrafish larvae exposed throughout their first stage and tested 7 days after hatching exhibit altered feeding behavior. When zebrafish and their food, the rotifers, *Brachionus calyciflorus* and *Lecane papuana*, were exposed to GBH at concentrations of 0.8 mg/L, zebrafish decreased their food consumption. However, zebrafish pre-exposed to GBH consumed non-GBH food at normal rates. Since zebrafish rely on olfactory cues to find food, the authors suggest that changes in tastes or smells caused differential feeding on exposed rotifers [134]. Fruit flies consume less medium containing Roundup® in a dose-dependent pattern [135]. Similarly, flies preferred an organic sucrose solution to a solution that contained Roundup® Ready to Use, a GBH formulation with the active ingredients glyphosate and pelargonic acid. However, they did not show a preference for the solution with Roundup® Super Concentrate, another GBH formulation containing the surfactant POEA and the active ingredient glyphosate, despite exposure to equal concentrations of glyphosate from both formulations. In the same study, flies given organic corn medium containing either Roundup® Ready to Use or Roundup® Super Concentrate at various concentrations later consumed more sucrose than those pre-fed with non-GBH medium. The authors attribute this to the flies consuming less of the GBH-contaminated medium, which prompted them to later consume more sucrose solution [136]. The spider, *Alpaida veniliae*, showed lower consumption rates when prey were exposed to GBH [137]. Effects of GBH exposure on honeybees are mixed. Newly emerged adult honeybees given food infused with glyphosate showed a decrease in food intake compared to the control [138,139]. However, a study conducted in the winter found honeybees consumed more food when it contained GBH at concentrations of 0.1, 1, and 10 µg/L. This study also combined other reagents with glyphosate such as glyphosate + insecticide Imidacloprid, glyphosate + fungicide difenoconazole, and glyphosate + imidacloprid + difenoconazole. The mixtures and individual reagents caused the honeybees to consume more food than the control [140]. Honeybees required higher concentrations of sucrose solution to elicit proboscis extension after GBH exposure [35,96,103,113]. Similarly, honeybees feeding on sucrose solution displayed no difference in food intake regardless of exposure [104,141–143] and broiler hens showed no preference between feed containing or without GBH [144].

Species pre-exposed to glyphosate demonstrated varying effects. The pacu fish, *Piaractus mesopotamicus*, displayed decreased food consumption after they were exposed to glyphosate. Pacu were exposed chronically (10–15 days) to glyphosate at 0.2, 0.6 and 1.8 ppm. While the details differed among days, fish exposed to all concentrations exhibited decreased feeding on at least some days. Those exposed to 1.8 ppm also exhibited such a decrease [145]. Pre-exposed freshwater planarian, *Girardia tigrina*, exhibited decreased food consumption as the concentration of Roundup® increased [146]. Another study tested how glyphosate and Roundup® exposure influenced larvae of the damselfly, *Coenagrion pulchellum*. The larvae were exposed to 1 mg/L or 2 mg/L, both of which led to an increase in consumption of food compared to the control [147]. Predator cues did not affect food consumption when larvae of the damselfly, *Enallagma cyathigerum*, were pre-exposed to 2 mg/L of glyphosate for seven days [148]. Adult and spiderling *Pardosa milvina* environmentally exposed to GBH Buccaneer Plus ate more crickets than unexposed controls. The authors attribute this behavior to hyperactivity from exposure to Buccaneer Plus [149]. A similar study involving both *P. milvina* and another wolf spider, *Tigrosa helluo*, also showed that Buccaneer Plus altered predator efficiency. Environmental exposure via paper discs saturated with 12 mL/m^2 GBH placed in random locations around the testing apparatus mimicked fields exposed to GBH. *T. helluo* were allowed to prey on crickets, *Acheta domesticus,* and on *P. milvina*; *P. milvina* were observed preying on crickets. In the presence of the herbicide, *T. helluo* were able to capture prey faster than the control for both prey types. While exposed and unexposed *P. milvina* did not differ in timing of predation, they required more lunges to capture their prey [150]. Another wolf spider, *Hogna* cf. *bivittata*, displayed pest-specific effects from GBH exposure, as they captured caterpillars and ants with lower efficiency than the control, but not when preying on crickets [151], while a different spider, *Pardosa agricola*, and the ground beetle, *Poecilus cupreus*, showed no significant difference in prey capture rates [152]. The water flea, *Daphnia pulex*, reduced grazing by 40% after pre-exposure at glyphosate concentrations of 50 mg/L [153]. Three-keeled pond turtle, *Mauremys reevesii*, eggs were exposed to glyphosate concentrations of 0, 2, 20, 200, and 2000 mg/L, which led to an increase in foraging time in the hatchlings at the two highest concentrations [154]. While some studies indicate that GBH exposure alters feeding behavior, others do not. For instance, in a study involving two predators, the southern hawker dragonfly, *Aeshna cyanae* and smooth newt, *Lissotriton vulgaris*, the predatory activity of organisms exposed to GBH, chronically or acutely, was no different from those unexposed, suggesting that GBH had no effect on the foraging of the predators [155,156].

Table 6. Effects of GBH in Food on Feeding Behavior.

Species	Herbicide/Ingredient Used	Concentration	Results	Source
Zebrafish (*D. rerio*)	Glyphosate	0.8 mg/L	Decrease in food consumption	[134]
Fruit fly (*D. melanogaster*)	Roundup®	1, 3.3, 10, 33 g/L	Decrease in food consumption	[135]
Fruit fly (*D. melanogaster*)	Roundup® Super Concentrate, Roundup® Ready to Use	0, 0.5, 1.0, 2.0 g/L, 10 g/L	Flies consumed less of the exposed food, consumed more food after exposed to GBH	[136]
Spider (*A. veniliae*)	Glifoglex® 48	192 mg/L a.i.	Lower consumption rates for prey exposed to GBH	[137]
Honeybee (*A. mellifera*)	Glyphosate formulation not listed	0, 2.5, 5 mg/L	No difference in food intake	[104]
Honeybee (*A. mellifera*)	Glyphosate	10 ppb, 100 ppb, 1 ppm, 10 ppm	No difference in consumption ratios except for the 10-ppb solution showing they consumed more	[142]
Honeybee (*A. mellifera*)	Glyphosate	2.5 mg/L	Honeybees showed decrease in food consumption	[138]
Honeybee (*A. mellifera*)	Glyphosate	0.1, 1, 10 µg/L	Food consumption increased in the presence of glyphosate	[140]
Honeybee (*A. mellifera*)	Credit Extreme® 240	1.25, 2.5, 5 ng/bee	Food consumption decreased over a 10-day period for food exposed to differing concentrations of glyphosate	[139]
Honeybee (*A. mellifera*)	Glyphosate	1.5, 7.5 mM	Food consumption did not vary for glyphosate in its isolated form or combined form with AMPA or Ncer	[143]
Honeybee (*A. mellifera*)	Glyphosate	75, 150, 301 a.e. mg/L	Glyphosate exposure did not alter food consumption	[141]
Broiler hen	Gallup super 360	47 mg Gly equivalent/kg body weight/day	No difference between exposure and post exposure to GBH	[144]

Table 7. Effects of Pre-Exposure to GBH on Feeding Behavior.

Species	Herbicide/Ingredient Used	Exposure	Concentration	Results	Source
Damselfly larvae (*C. pulchellum)*	Glyphosate and Roundup®	Individuals	1, 2 mg/L	Increase in food consumption	[147]
Damselfy larvae (*E. cyathigerum*)	Glyphosate	7 days	2 mg/L	Increase in food consumption	[148]
Southern hawker dragonfly (*A. cyanea)* Smooth newt (*L. vulgari)*	Glyphogan Classic	Mesocosm exposed	6.5 mg/L	No visible effect	[155,156]
Wolf spider (*P. milvina)*	Buccaneer Plus	Testing apparatus exposed	9 a.e. g/L	Captured more prey than control	[149]
Pacu (*P. mesopotamicus)*	Unspecified glyphosate formulation	Fish exposed	0.2, 0.6, 1.8 ppm	Food consumption decreased exposure	[145]
Water flea (*D. pulex*)	Pure glyphosate	Organism exposed	50 mg/L	Reduced grazing	[153]
Wolf spider (*T. helluo* and *P. milvina*)	Buccaneer Plus	Paper filter discs were exposed with herbicide	12 mL/m^2	*Tigrosa* caught prey faster while *P. milvina* required more lunges to capture prey	[150]
Three-keeled pond turtle(*M. reevesii*)	Glyphosate—ammonium	Eggs were exposed	0, 2, 20, 200, 2000 mg/L	Increase in the amount of time it took to forage	[154]
Wolf spider (*H.* cf. *bivittata*)	Unspecified glyphosate formulation	In a test tube 30 min	280 mg/L a.i.	Lower consumption rates for specific prey	[151]
Planarian (*G. tigrina*)	Roundup ®	GBH 96 h	1.87, 3.75, 7.5, 15 mg/L a.e. glyphosate	Decrease in consumption rates as concentration increased	[146]
Agrobiont spider (*P. agricola*) Ground beetle (*P. cupreus*)	Roundup ® Biaktiv	Freshly doused paper and paper left to dry for 1 day		No significant difference in predation rates	[152]

3.3. Anti-Predator Behavior

Glyphosate-based herbicides like Roundup® have adverse effects on anti–predator capabilities of some organisms, but not others (Table 8). For some organisms, exposure to GBHs led to a decrease in predator awareness. Zebrafish exposed to GBH were found to be in areas that put them at a higher risk of predation indicating loss in predator awareness compared to unexposed fish [157–161]. In another fish, the common spiny loach, *Lepidocephalichthys thermalis*, exposure to Roundup® (3 h and 15 days at 0.8 mg/L) led to an increase in activity in the presence of conspecific alarm cues (CC) [162]. Wood frog, *Lithobates sylvaticus*, tadpoles exposed to injured conspecific cues and Roundup® did not change their activity, while tadpoles unexposed to Roundup® decreased activity when exposed to cues from injured conspecifics, which indicates that glyphosate impairs the tadpole's ability to respond to the threat of predation [163]. Gulf coast toad, *Incilius nebulifer,* tadpoles pre-exposed to Roundup® and exogenous corticosterone (CORT) became more active in the presence of predator cues. Pre-exposure to the individual reagents and control all showed a decrease in activity [164]. Blue Ridge two-lined salamander showed synergistic effects of temperature and glyphosate on anti-predator behaviors. Use of refuge became less frequent in exposed salamanders at ambient temperatures (12 °C) and an interactive effect between elevated temperatures (23 °C) and glyphosate also had lower frequency of refuge use. Glyphosate led to a reduction in burst distance, speed and distance from a predator attack, unaffected by temperature [127]. When exposed to Roundup®, damselfly larvae exhibited more activity in the presence of predator cues than the controls, which reduced their activity in the presence of predator cues. Exposed larvae walked more, faced their food and fed more often than the controls. However, the predator, the emperor dragonfly, *Anax imperator*, was not more effective at eating exposed larvae than the controls, despite the change in anti-predator behavior, perhaps because exposed larvae's increased swimming speeds may counteract the reduced anti-predator behavior [165]. In damselfly, exposure to either Roundup® or pure glyphosate at 1 or 2 mg/L induced slower escape speeds in the presence of predator cues. Roundup® induced significantly slower escape speeds than glyphosate, indicating that "inert" ingredients affected their anti-predator capabilities [147]. Exposure to GBH decreased the amount of time wolf spiders spend ambulatory compared to controls in response to predator cues from beetles but not giant wolf spiders' predator cues [166].

In other organisms, exposure to GBH causes little to no effects on anti-predator behavior. For instance, threat of predation from newts and dragonflies did not affect the anti-predation behavior of tadpoles of the agile frog, *Rana dalmatina*. Tadpoles exposed to varying levels of herbicide exhibited different behaviors, as the concentration increased, tadpoles decreased their activity around the predators. It was also shown that more tadpoles hid more often at the higher concentrations from the predators, more tadpoles hid from the dragonfly larvae than newts. Overall, the authors suggest that exposure to the herbicide did not significantly alter the tadpole's anti-predator response [167]. Likewise, the anti-predator capabilities of marsh frog tadpoles were not affected by exposure to Roundup® Power 2.0 [130].

Table 8. Effects of GBH exposure on anti-predator behavior.

Species	Herbicide/Ingredient Used	Exposure	Concentration	Results	Source
Zebrafish (*D. rerio*)	Roundup®	Exposed for 30 min	1.4 µL	After simulated bird attack, fish remained in the central zone compared to control and other tests.	[157]
Zebrafish (*D. rerio*)	Roundup®	Exposed from 3–120 h post fertilization	4.8 µg/L	Exposed fish remained in the area which had a stimulus unlike control; exposed fish displayed hypermobility and more time spent in the central zone	[158]
Zebrafish (*D. rerio*)	Glyphosate	Exposed from 3–120 h post fertilization	4.8 µg/L	After predatory stimulus, fish entered and spent more time in the central zone than the control	[159]
Zebrafish (*D. rerio*)	Roundup®	Pre-exposed for 96 h	3, 5 mg/L	Exposed fish spent more time spent in the top zone of the tank compared to the bottom zone	[160]

Table 8. *Cont.*

Species	Herbicide/Ingredient Used	Exposure	Concentration	Results	Source
Zebrafish (*D. rerio*)	Roundup® Ultramax	Embryos were pre-exposed for 72 h	0, 1, 2, 5 µg a.i./mL	5 µg a.i./mL led to less time spent at the bottom of the tank when a visual stimulus was encountered, indicating loss of fear	[161]
Common spiny loach (*L. thermalis*)	Roundup®	Pre-exposed for 3 h and 15 days; briefly exposed to Roundup® mixed with CC and other mixtures	0.8 mg/L	Pre-exposure led to an increase in activity in the presence of conspecific alarm cues (cc); unexposed fish did not detect conspecific alarm cues when Roundup®+cc were mixed	[162]
Wood frog tadpoles (*L. sylvaticus*)	Roundup® weathermax	Tadpoles were pre-exposed for 1 h; unexposed tadpoles briefly exposed to CC mixed with Roundup® and other mixtures	0.5 mg a.e./L	Pre-exposure led to no change in behavior in the presence of conspecific cues compared to control; unexposed tadpoles exposed to Roundup® mixed with CC led to no change in behavior compared to control suggesting Roundup® inactivated CC	[163]
Gulf coast toad tadpoles (*I. nebulifer*)	Roundup® ready to use	Tadpoles were pre exposed for 7 days	0.736 mg a.e/L	Mixture of Roundup® and exogenous corticosterone led to more activity compared to individual reagents and control	[164]
Blue Ridge two-lined salamander (*E. wilderae*)	Roundup® ready to use	Exposed for 5 h.	0.73, 1.46, 2.92 µg a.e./L.	Ambient temperatures + glyphosate led to a lower frequency of refuge as the concentration increased; reduction in burst speed (speed and distance away from a predator) occurred during exposure	[127]
Damselfly larvae (*E. cyathigerum*)	Roundup®	Pre-exposed for 24 h	1.5 mg/L	Exposure led to more activity in the presence of predator cues compared to the control; survival rate from altered anti-predator behavior did not have a significant change on survival from predation	[165]
Damselfy (*C. pulchellum*)	Roundup® and glyphosate	Pre-exposed for 7 days	1, 2 mg/L	Exposure to glyphosate and Roundup® led to a decrease in escape swimming speed with 2 mg /L of Roundup® inducing the slowest escape speed	[147]
Wolf spider (*P. Milvina*)	Buccaneer Plus	Semicircles were sprayed with herbicide and placed in testing apparatus.	2.5%	Exposure led to less time moving when exposed to *S quadriceps* cues but not to *H. Helluo*	[166]
Agile frog (*R. dalmanita*)	Glyphogan classic	21 days of exposure	0, 2, 6.5 mg a.e./L	Increase in concentration led to a decline in activity in the presence of predators, except for newts which were similar to the control (no predator); hiding occurred more often at higher concentrations, except for newts and the control	[167]
Marsh frog tadpoles (*P. ridibundus*)	Roundup® power 2.0	Embryos were exposed for 96 h	0.7 mg a.e./L, 3.1 mg a.e./L and 7.6 mg a.e./L	Exposure had no effect on anti-predator behavior	[130]

3.4. Reproductive and Maternal Behavior

As an endocrine disruptor, glyphosate and GBHs particularly affect animal reproduction and reproductive behavior. Exposure to glyphosate can lead to a variety of negative effects on the reproductive systems of animals, including courtship, mating, fertility, and maternal behavior (summarized in Tables 9 and 10). Ait Bali et al. [106] found that the mice had difficulty conceiving and success rates rapidly declined when exposed to higher concentrations of glyphosate. The females who were not exposed to glyphosate had an 87% success rate for conceiving, females exposed to 250 mg/kg had a 60% success rate, and females exposed to 500 mg/kg had a 25% success rate. Similarly, fecundity rates and fertility rates of planaria decrease as the concentration of glyphosate increases [146]. In earthworms, *L. terrestris* and *Aporrectodea caliginosa*, and Japanese medaka, *Oryzias latipes*, it was found that fecundity and fertility rates were negatively impacted by GBH exposure [168,169]. The offspring of female Wistar rats exposed to GBH had lower rates of fertility as well [170].

Pinning behavior, considered crucial for the development of sexual competence in males, was diminished in both male and female offspring perinatally exposed to the highest dose of GBH. Both doses of GBH reduced female sexual behavior, as demonstrated by a decrease in the female's receptiveness to the male's sexual advances, measured by latency to the first lordosis, a postural change in females that indicates receptivity to mating, number of lordosis, and number of mounts without lordosis. Male sexual behavior, measured in latencies to the first mount, first intromission, first ejaculation, number of total mounts with or without intromissions, and number of ejaculations in 30 min, was unaffected. The study suggests that the prenatal and lactational exposure to GBH disrupted aromatase activity, leading to the impairment of sexual behavior in female offspring, including a precocious vaginal opening [171].

GBHs decrease masculinization of male mice exposed before puberty [172,173]. Both maternal exposure to glyphosate and exposure before puberty disturbed the masculinization process during the critical period of sexual hypothalamic differentiation. Sexual partner preference score, measured by (total time spent in estrous female area—total time spent in sexually active male area), increased and copulatory behavior was altered, with an increase in latency to first mount, first intromission, and mount after first ejaculation. In the same mice, exposure increased estradiol serum concentrations, but this did not lead to increased sexual arousal. However, the mice began puberty at a younger age, which may lead to an increase in sexual behaviors at a younger age [172].

Wolf spider males exhibit less courtship when exposed to glyphosate. Females were placed inside traps and 47.2% of the traps captured between one and four males. Traps with GBH on filter paper inside the trap captured fewer males than those treated with distilled water. Traps with GBH surrounding the opening also captured fewer males than those with only water on the filter paper ring. This suggests that the herbicide interferes with female pheromone production. In an olfactometer experiment, there was no significant difference in the choice of a corridor that the spider took regardless of the presence of a female or not, leading to belief that the spiders were not repulsed by GBH itself. The conclusion was made that the males had trouble in detecting and/or responding to the females pheromones [174]. Another study confirmed that exposure to glyphosate impaired sexual chemical communication between female and male wolf spiders, *Pardosa agrestis*, reducing the male spider's ability to find their mate [175]. Male agrobiont spiders and beetles exhibit similar courtship behaviors and experience similar success rate and duration of mating regardless of whether the surface they were on contained GBH residues [152]. A similar study on wolf spiders and glyphosate showed no significant effect on courtship or sexual behavior in either sex of the spider [176]. This may be due to differences between species. While exposure levels from [176] are difficult to compare because of different experimental procedures (5.04 $\mu g/cm^2$ at 30.34%), they appear to be comparable among the other three studies (12 g/L [174], 14.4 g/L [152] and 15 mL/L [175]).

Chronic sublethal exposure to glyphosate and another pesticide, thiacloprid, negatively affected colonies of the ant species, *Cardiocondyla obscurior*, decreasing the number of eggs and pupae when exposed to both pesticides simultaneously [177]. Specifically, queens' reproductive performance decreased, possibly due to trade-offs between detoxification and reproduction. The density of endosymbionts in workers decreased, which could be responsible for the decrease in the queens' reproductive performance. In addition, the pesticides had no effect on the sex ratio, but resulted in smaller colonies. The results highlight the importance of studying multiple stressors and the long-term effects of chronic exposure.

Exposure to glyphosate and its commercial formulations can interfere with the reproductive fitness of fish by affecting their neural and endocrine systems. Exposure to glyphosate (0.5 mg/L in Roundup$^{®}$) decreases the sexual activity and sperm quality of male livebearers found in rice plantations in southern Brazil and northern Argentina [38,126]. Livebearers also experienced a reduction in copulation and mating success, thus decreasing sexual activity [178]. GBH exposure also negatively impacts mate attraction by changing territorial behavior, aggressiveness, and coloration of livebearers, zebrafish, and male Mozambique tilapia, *Oreochromis mossambicus*, all traits important in courtship behavior and mate attraction, which ultimately decreases reproduction. Territorial behavior is important because females lay their eggs within these territories, and those with more resources attract more females. Aggressiveness includes chasing and biting rival males to secure access to females. Finally, coloration indicates a male's health and genetic quality, such that brighter and more colorful patterns attract females [178,179]. Adult zebrafish that are exposed to glyphosate in combination with warm temperatures showed significant malformities in offspring, which may ultimately negatively impact sexual development and behavior in later stages of life [180]. Conversely, GBH exposure did not significantly impact the fertility and reproductive potential of rainbow trout, since both the control and exposed fish had high fertility [129]. GBHs decreased ovary size and number of mature oocytes in fruit flies [181], which may account for GBH-induced reductions in fertility [61].

Several studies [106,171,182,183] show that female rats and mice who were exposed to glyphosate while pregnant exhibited less maternal behavior, including decreased nursing, grooming of offspring, brooding, and reduced time spent in the nest compared to unexposed pregnant females. This negatively affects the offspring, interfering with their development and interactions with their environment. For example, offspring of exposed mothers had reduced locomotor function and mental health impairments. It was also found that maternal exposure to GBH had negative effects on maternal care of offspring, resulting in decreased body weight of rats at 75 and 90 days of age, with male offspring being more susceptible than females [171]. Another study [184] found that perinatal exposure to GBH reduced maternal care and aggressive behavior in rats, which may impair their ability to protect their offspring from predators. This was due to hormonal deregulations that decreased maternal reflexes and motivation. The time and number of pups retrieved decreased with a high dose of GBH, and maternal grooming and nesting was also observed to decrease. Maternal grooming and nesting are important for the pups' development of endocrine and emotional responses to stress, and the lack of such grooming or nesting by the mother can alter the pup's endocrine development and its response to stress later in life.

Maternal behavior of Wistar rats exposed to two different concentrations of GBH during pregnancy and lactation was not affected, nor did it impact water and food intake of mothers or their body weight, gestational length, or litter size. There were also no visible external malformations in the pups or any effect on their body weight due to GBH intake by mothers. These findings suggest that exposure to GBH during pregnancy and lactation did not have any significant adverse effects on maternal behavior of rats [185]. No significant changes were observed in maternal behavior of Wistar rats between the experimental and control groups [183]. These conflicting results may be attributed to the lower doses of GBH in both Gallegos [185] and de Oliveira [183] and the different formulations that were used. Additionally, there were no observed behavioral changes in Japanese medaka fish despite induced altered expression in reproductive related genes [169].

Nikbakhtzadeh and Fuentes [186] found that exposure to glyphosate was lethal to eggs, larvae and pupae, prolonged larval development, and delayed pupation of the mosquito, *Culex quinquefasciatus*. Female mosquitoes avoided ovipositing in glyphosate-contaminated water [186], but glyphosate at 5 mg/L from Roundup® Super Concentrate had no effect on where female field crickets, *Gryllus lineaticeps*, chose to lay their eggs [187].

Table 9. Effects of GBH exposure on courtship and mating behavior.

Animal	Behavior	Exposure	Test Used	Outcome	Source
Swiss mice, male and female	Courtship	In food: glyphosate 250 mg/kg and 500 mg/kg	Copulation, fertility, and fecundity rates	- Higher rates of copulation with low fertilization success rate as concentration of glyphosate increased	[106]
Mozambique tilapia (*O. mossambicus*), male and female	Courtship	5 ppm, 8 ppm and 10 ppm of glyphosate	Color pattern, chasing distance of males, chasing occurrences, size of territory	- Negatively impacted color and pattern of fish. - Higher concentrations of GBH reduced the distance males chased their rivals and effects leveled off after 8 ppm - Chasing occurrences decreased from control to experimental, however, experimental groups were not significantly different from each other - Territory sizes decreased from control to experimental group. 8 ppm and 10 ppm concentrations showed no significant difference from one another	[179]
Planarian (*G. tigrina*) male and female	Fertility	Borosilicate glass beakers: Roundup® Original 1.87, 3.75, 7.5 and 15 mg a.e./L	Fertility and Fecundity rates	- Decreased fertility	[146]
Rainbow trout (*O. mykiss*)	Fertility and fecundity	360 and 420 g/L Glyphosate	Fertility and Fecundity rates	- No significant difference between control and experimental when it came to fertility and fecundity rates	[129]
Earthworm (*L. terrestris* and *A. caliginosa*)	Fertility and fecundity	Unspecified concentration of GBH	Fertility and fecundity rates	- Fertility and fecundity both decreased when GBH was introduced.	[168]
Male wolf spider (*P. milvina*)	Courtship behavior	Roundup® II Original diluted to 12 g/L	Olfactometer experiment and pitfall experiment	- GBH made it difficult for the male spiders to find their mates	[174]
Livebearer (*J. multidentata*), male and female	Courtship behavior	Roundup®: 5, 10, 20, 35, 60, and 100 mg/L	Number of persecutions, copulation attempts, number of copulations, and mating success	- Lower number of copulations in the fish exposed to GBH - Mating success dramatically decreased in the males that were exposed to GBH after 28 days	[178]
BALB/c mouse, male and female	Courtship behavior	Roundup® Transorb: 50 mg/kg of glyphosate	Open-field test, elevated plus-maze test, and forced swim test	- Male mice exposed to glyphosate before puberty had a demasculinization effect.	[173]
Wolf spider (*P. agrestis*)	Courtship behavior	15 mL/L of Roundup® and 3 mL/L of Nurelle D	Two-choice olfactometer and Y-maze set-up	- Males were less likely to follow the females 3 h after a one-time exposure to the environment that the females were kept. Sexual chemical communication was disturbed	[175]
Ant (*C. obscurior*)	Fertility	fed with 75% honey-water mix-ture containing 3 µg/g thiacloprid, 100 µg/g glyphosate or 3 µg/g thiacloprid+ 100 µg/g glyphosate	Egg production, pupae production	- Decreased brood production and decreased reproduction in the queen ant observed in combination treatment of thiacloprid and glyphosate.	[177]
Many fish species from embryo to adult	Courtship	Many different concentrations of glyphosate	Many different tests done from each paper	- Decreased sexual activity and aggresivness	[38]

Table 9. *Cont.*

Animal	Behavior	Exposure	Test Used	Outcome	Source
Agrobiont spider (*P. agricola*), ground beetle (*P. cupreus*)	Courtship	Roundup® Biaktiv Diluted to 1 part GBH and 25 parts water (1:25) = 14.4 g/L	Predation, locomotion, Avoidance, defence, and mating	- No significant difference between control and experimental group in sexual behaviors	[152]
Wistar rat, male and female	Fertility	MAGNUM SUPER II, 2 mg/kg/day or 200 mg/kg/day	Fertility rates	- Impaired reproductive capability in the F1 generation	[170]
Fruit fly (*D. melanogaster*)	Fertility	Roundup® Super Concentrate: 0.5, 1.0, and 2.0 g/L and Roundup® Ready to Use: 1.0, 2.0, and 4.0 g/L	Ovary size, number of mature oocytes, body weight of females	- Reduced size of ovaries and reduced number of mature oocytes	[181]
Mosquito (*C. quinquefasciatus*)	Fertility	Roundup® super concentrate: 0.5 and 1 g/Liter	Oviposition experiment, egg viability experiment, and triple-choice oviposition experiment	- Females avoided ovipositing in GBH exposed waters	[186]
Wistar rat, male and female	Courtship	Roundup® Transorb: 50 and 150 mg/kg	Observations on male and female sexual behavior	- No significant change in behavior in male rats in experimental and control groups - Reduced sexual behavior; treated offspring showed increased latencies to the first lordosis and reduced number of lordosis compared to the control group. No difference in the number of mounts between both groups	[171]
Wistar rat PND 90 and adult	Courtship	Roundup® Transorb: 0.25 mL/ 100 g of body weight between 7 and 8 am from GD18 to PND5	Sexual partner preference score, sexual behavior	- Males exposed to GBH spent more time in the females' section and copulatory behavior was altered - Sexual partner preference in males exposed increased approximately 4-fold towards females - Puberty was seen starting at a younger age	[172]
Japanese medaka (*O. latipes*)	Courtship	Embryos exposed to 0.5 mg/L glyphosate, 0.5 mg/L and 5 mg/L Roundup® for 15 days	Fecundity and fertilization efficiency	- Induced altered expression in reproductive related genes; however, no effect on behavior	[169]
Zebrafish (*D. rerio*)	Fertility	1 ppm and 5 ppm glyphosate for 96 h temperatures: 28.5 °C, 29 °C, 29.5 °C, and 30 °C		- Parents who are exposed to glyphosate and high temperatures have offspring who are malformed which ultimately affects sexual development and activity later in development	[180]
Fruit fly (*D. melanogaster*)	Courtship	Roundup® sprayed on GMO corn and then fed to fruit fly	Portion mated (females) and courtship rate (males)	- No significant changes in behavior when flies were exposed to Roundup®or GMO corn - Mortality and reproduction were significantly impacted even in the lower end of dosage used in the experiment.	[61]
Wolf spider (*P. milvina*)	Courtship	Hi-Yield® Kilzall 5.040 µL/cm^2	Body shakes and leg raises	- No change in courtship or mating behavior	[176]

Table 10. Effects of GBH exposure on maternal behavior.

Species	Exposure	Behavior	Outcome	Source
Swiss mice, male and female	In food: glyphosate 250 mg/kg and 500 mg/kg	Nest building	- Decreased nest building	[106]
Sprague Dawley Rat, male and female	Vanilla wafer cookie: Glyphosate: 5 mg kg^{-1} d^{-1} and Roundup® Plus: 5 $mgkg^{-1}d^{-1}$	Maternal behavior	- Mothers exposed to GBH spent more time licking their pups	[182]
Wistar rat, male and female	Glifloglex®: 0.65 g/L and 1.30 g/L	Maternal Behavior	- No significant change in maternal behavior while rats were pregnant	[185]
Wistar rat, male and female	50 mg/kg per day of GBH	Maternal behavior	- No change in maternal behavior between both experimental and control groups	[183]
Wistar rats, male and female	Roundup® Transorb: 50 and 150 mg/kg of GLY-BH	Pup retrieval, percentage of dams that retrieved all pups, total number of pups retrieved for each dam, grooming of the pups, fullmaternal behavior, nest building, maternal aggressive behavior	- Mothers treated with 150 mg/kg GBH had impaired maternal aggressive behavior - The mothers exposed to glyphosate showed a decrease in maternal behavior through an increased pup-retrieval time, a decrease in the number of pups retrieved, and a decrease in maternal grooming - Decrease in nesting and full maternal care in rats exposed to glyphosate	[184]
Cricket (*G. lineaticeps*)	Roundup®: 5 mg GLY/L of water and glyphosate: 5 mg/L of water	Choice oviposition experiment and no-choice oviposition Experiment	- Neither herbicide affected where the mothers oviposited	[187]

3.5. Learning, Memory, and Cognition

Learning involves the acquisition of new information, while memory is the ability to retain that information and apply it in future situations. Studies that focus on visual and olfactory learning tasks indicate that some sensory learning systems are extremely susceptible to GBH exposure, while in other situations they may not be affected at all (Table 11). In the mosquito, *Aedes aegypti*, for example, habituated less to a visual stimulus after exposure to a dose only 5% of the lethal dose, and almost completely lost habituation at higher but still field-relevant concentrations [188]. The effect of GBH on honeybee sensory learning is more complicated. In two-color discrimination associative learning, whether the association was between neutral stimuli and electric shock [100] or between a sucrose reward and an aversive solution [189], GBH exposure did not affect visual learning. However, in a 10-color discrimination scenario, which is a realistic foraging situation for honeybees, GBH-exposed bees failed to learn during the second half of training, resulting in significantly worse performance than unexposed control bumblebees, *Bombus terrestris* [189]. The same authors found no effect on 10-odor discrimination. Glyphosate exposure did impair olfactory learning in 9-day-old young adult honeybees (but not at 5 or 14 days, [138]) and adult honeybees [98,104] in some two-choice associative learning situations, but not in another [190]. Apparently, difficult sensory learning tasks are more likely to be damaged by GBH exposure than simple ones.

Even in paradigms in which sensory learning is not impaired by GBH exposure, memory often is (Table 12). Though Hernandez et al. [190] found no effect on learning, or on memory overall, exposure did shorten memory retention from long-term to medium-term sensory memory. Helander et al. [189] found that sensory memory was significantly and strongly impaired in the same situations as learning and 10-color discrimination but not 2-color or 10-odor situations. Importantly, this was true whether bees were exposed to GBH before or after learning acquisition. Similarly, Herbert et al. [104] and Luo et al. [98] identified deficiencies in short-term and medium-term olfactory memory in exposed honeybees. A study of farmers in Uganda identified that visual memory is also impaired by pesticide exposure in humans, as are language memory, perceptual motor function, complex attention, and processing speed. Specifically, glyphosate exposure is associated with impaired visual memory, as measured by the Benton visual retention test [191].

Spatial learning ability has been assessed based on maze completion in rats and turtles, and homeward flight paths in honeybees. In an open field experiment, honeybees exposed to GBH took longer to accomplish homeward flight, and were less likely to transition from an indirect flight path on their first trial to a direct path on the second [99]. Similarly, turtles exposed to GBH took longer to complete a cross maze, and those exposed to high concentration took longer than low concentration [154]. Rat spatial learning was examined using the Morris Water Maze test, where they use visual cues outside of the water to find a submerged platform in opaque water. Those rats exposed to GBH took longer to find the correct quadrant and the platform during the second half of the learning phase, regardless of the exposure concentration [192].

GBH exposure impaired spatial memory even more strongly than spatial learning. In honeybees, those exposed to GBH at 25% or 50% of the ED_{50} (ED_{50} = 10 mg/L in sucrose) concentration took 6 or 10 times longer to complete a simple maze 2 h after training than unexposed controls. After 24 h, the results were only slightly less pronounced. In addition, while control bees required no course corrections, exposed bees did in a dose-dependent manner. Differences between exposed and unexposed bees were even greater in a complex maze, both in terms of completion time and course corrections [60], again indicating that more complex types of learning and memory decrease more than simple ones. Rodents' spatial memory was also impaired, including rats tested in the water maze test mentioned above [192] (but not [193]). In addition, chronic GBH exposure reduces short term spatial memory in a y-maze among young mice exposed through maternal dosing, prenatally, and through lactation [106] (but not those exposed only during gestation [194]) and chronically exposed adult mice [195].

Mice and rats explore and spend more time with an unfamiliar (novel) object than one they have spent time interacting with in the past. However, mice exposed to GBH fail to discriminate between novel and familiar objects. In adults, chronic and subchronic exposure significantly reduce discrimination. This effect most prominently impacts short-term (6-h) memory [107]; and is dose-dependent when young mice are exposed through maternal dosing [106]. These results are similar in rats, both in terms of an increase in variance among exposed females and overall novel object recognition impairment in males [196] or both sexes [192]. In contrast, Del Castilo et al. [193] did not observe a decrease in novel object recognition in 3-month-old mice exposed to GBH since pregnancy; the difference may be attributed to lower doses.

Consistent GBH exposure is detrimental to aversive stimulus-avoidance memory in mice and in fish. In both taxa, electric shocks are applied when the animal enters a dark area of their arena during training. Short-term memory is measured as the latency to enter the dark area 2 h later; long-term memory is tested 24 h after training. Mice exposed to 500 mg/kg, whether as adults [195] or through maternal dosing [106] exhibited shorter latency to enter the dark area after 24 h, whether dosing was chronic, subchronic or acute. Maternally dosed and chronically dosed adults' short-term avoidance memory was also impaired at this dose. A lower dose of 250 mg/kg impaired avoidance memory after acute and subchronic dosing in adults (short-term memory), subchronic and chronic dosing in adults (long-term memory), and maternal dosing (long-term only). In zebrafish [115] and a livebearer fish [126], long-term aversive stimulus memory is impaired by GBH exposure. These are also among the few learning and memory papers that directly compare exposure to different formulations. Consistent with results from a wide variety of taxa comparing the effects of glyphosate to those of formulated GBHs on many different behavioral, physiological, morphological, and genetic endpoints (reviewed in [28,56]), Bridi [115] found that Roundup® exposure affected memory more than exposure to glyphosate alone, and Sanchez et al. [126] compared two different Roundup® formulations with somewhat different results.

Most information about how GBH exposure affects humans is based on case studies resulting from accidental acute exposure or intentional exposure during suicide attempts. Most of these case studies indicate that short-term and/or verbal memory loss occurs. The exception is Wang et al. [75], who report a case in which the patient exhibited parkinsonian syndrome, but without short-term memory loss. Other cases do report short-term memory loss, often beginning quickly (hours to days after exposure) [95,197,198]. In some cases, memory loss lasted for many months [95] or years [199] through the end of the study. In other cases, dramatic improvements were observed [197,198]. Types of memory affected include word recall [197], confusion, verbal memory, general memory and delayed memory [95], and both retrograde and anteriograde amnesia [95,198]. While there is some variation among these case studies, both in how patients were assessed and the memory impairments reported, the overall pattern indicates that short-term and language memory are most often affected.

Table 11. Effects of GBH exposure on learning.

Animal	Exposure	Specific Behavior	Behavior Test Used	Behavioral Outcomes	Source
Rat pups PND 28–35	Glyphosate 35 mg/kg 70 mg/kg every 2 days PND 7–27	Spatial learning	Morris water maze test	Learning less at days 3 and 4	[192]
Honeybee (*A. mellifera*)	Glyphosate PESTANAL 2.5 mg/L 5 mg/L 10 mg/L	Spatial learning	Homeward flight path	Proportion direct second trial > first trial in controls (3/15 vs. 12/15) but not exposed bees (8/16 vs. 11/16) Proportion with indirect on the first trial →direct on second decreased with concentration but not significant	[99]
Honeybee (*A. mellifera*)	Roundup® or glyphosate 0.12 mg/L (1.2 ng/bee) 0.24 mg/L (2.4 ng/bee) 2 weeks of sucrose solution	Aversive stimulus learning, visual learning	Associative learning task: 2-color choice paired with shock	No effect	[100]
Honeybee (*A. mellifera*) young bees	Glyphosate	Associative olfactory learning	Training: olfactory stimulus paired with reward, vs. unpaired	5 days old: no effect 9 days old: impaired 14 days old: no effect	[138]
Bumblebee (*B. terrestris*)	Roundup® Gold 0.1 µL once before training	Associative visual learning	10-color choice paired with sucrose reward or aversive solution	Untreated bees increased performance during each of the five bouts. Treated bees failed to learn between 3 and 4, or 4 and 5 and performed significantly worse than controls during 4 and 5	[189]
		Associative visual learning	2-color choice	No effect	
		Associative olfactory learning	10-odor choice	No effect	
Honeybee (*A. mellifera*)	Glyphosate 2.5 mg/L 5 mg/L Daily, 15 days	Associative olfactory learning	Proboscis extension response (PER)	Sucrose sensitivity, elemental and non-elemental learning impaired	[104]
Honeybee (*A. mellifera*) adult foragers	Glyphosate 375 ng 1500 ng Single dose or divided over three days	Associative olfactory learning	PER	No effect	[190]
Honeybee (*A. mellifera*)	Roundup®, unspecified formulation 0.72 g/L 3.6 g/L = recommended dose7.2 g/L 3 h/day, 11 days	Associative olfactory learning	PER	%PER lower in bees exposed to paired sucrose and odor during 2nd and 3rd conditioning sessions for ½ RC and 2 RC but not 1 RC	[98]
Honeybee (*A. mellifera*)	ED$_{50}$ = 10 mg/L, ED$_{25}$ = 5 mg/L dissolved Roundup® granules in saturated sucrose solution administered 2 h before testing	Spatial learning	Simple maze completion time	>10× longer for ED$_{50}$ and >6× longer for ED$_{25}$ bees to complete	[60]
			Complex maze	Even greater differences in completion time and course corrections (though control bees did make course corrections, exposure increased >10×	
Mosquito (*A. aegypti*) fourth-instar larvae (5–8 days from hatching)	Glyphosate from hatching	Non-associative visual learning	Habituation to shadow	Decreased by doses <5% of lethal dose 50 µg/L—no effect, normal habituation 100 µg/L—intermediate 210 µg and 2 mg/L—almost no habituation	[188]

Table 12. Effects of GBH exposure on memory.

Animal	Exposure	Specific Learning/Memory Behavior	Behavior Test Used	Behavioral Outcomes	Source
Swiss mice male 1 month	GBH, unspecified formulation 250 or 500 mg/kg/day: acute (once); subchronic (daily for 6 weeks); chronic (daily for 12 weeks)	Recognition memory	Novel object recognition	Chronic and subchronic—reduced discrimination Acute—similar average discrimination ability (NS), more variation	[195]
		Spatial working memory	Y-maze	Chronic—reduced spontaneous alternation Subchronic—no effectAcute—no effect	
		Aversive stimulus memory	Passive avoidance task	Short-term memory (2 h): chronic—500 mg/kg reduced latency subchronic and acute—250 mg/kg reduced latency Long-term memory (24 h): chronic and subchronic—250 and 500 mg/kg reduced latency acute—500 mg/kg reduced latency	
Swiss mice male and female offspring 60+ days	GBH, unspecified formulation 250 or 500 mg/kg/day: maternal gestation and lactation	Working memory	Y-maze	Lower alternation in a dose dependent manner	[106]
		Recognition memory	Novel object recognition test	Reduced ratio of time with novel object in a dose-dependent manner Lower discrimination index	
		Aversion avoidance memory	Passive avoidance test	Short-term memory (2 h): decreased latency at 500 mg/kg Long-term memory (24 h): decreased latency at 250 and 500 mg/kg	
Mice male 4 weeks	Glifloglex® 4 mg/day 3X/wk, 50 mg/kg/day: intranasal	Recognition memory	Novel object recognition test	Short-term (6 h): impaired Long-term (24 h): not impaired (recovered)	[107]
Swiss mice male and female 3 months	Roundup®, unspecified formulation 0.075% *w*/*v*: Drinking water	Recognition memory	Novel object recognition test	No differences for males or females	[193]
		Spatial memory	Water maze	No difference for males or females	
Rats male and female adults	Glifloglex® 0.65 g/L (NOAEL; 100 mg/kg/day) 1.3 g/L (200 mg/kg/day) gestation and lactation	Recognition memory	Novel object recognition test	Females—no significant effect; high variation among exposed females during familiarization phase Males—impaired	[196]
Rat pups PND 28–35	Glyphosate 35 mg/kg 70 mg/kg every 2 days PND 7–27	Recognition memory	Novel object recognition test	Decrease in time spent with novel object at both concentrations	[192]
		Spatial memory	Morris water maze test	Lower in rats exposed to either concentration	
Bumblebee (*B. terrestris*)	Roundup® Gold 0.1 µL once before training	Associative Visual memory	10-color choice paired with sucrose or aversive solution	Whether treated before learning bout 1 or after learning bout 5, exposed bees performed significantly and much worse than control bees	[189]
		Associative Visual memory	2-color choice	No effect	
		Associative Olfactory memory	10-odor choice	No effect	

Table 12. *Cont.*

Animal	Exposure	Specific Learning/Memory Behavior	Behavior Test Used	Behavioral Outcomes	Source
Honeybee (*A. mellifera*)	Glyphosate 2.5 mg/L 5 mg/L Daily, 15 days	Associative olfactory memory	Proboscis extension response (PER)	Short-term memory decreased	[104]
Honeybee (*A. mellifera*) adult foragers	Glyphosate 375 ng 1500 ng Single dose or divided over three days	Associative Olfactory learning	PER	memory retrieval at 14 min or 24 h after conditioning did impair memory retention patterns—unexposed bees were more likely to have successful long term than medium term memory, while exposed bees were more likely to have successful medium term memory.	[190]
Honeybee (*A. mellifera*)	Roundup®, unspecified formulation 0.72 g/L 3.6 g/L = recommended dose 7.2 g/L 3 h/day, 11 days	Associative Olfactory learning	PER	% PER lower for all exposed bees in memory trials 1–5, but only significant for 1/2RC in all trials and in T1, T4, and T5 for 1RC	[98]
Honeybee (*A. mellifera*)	ED_{50} = 10 mg/L, ED_{25}= 5 mg/L dissolved Roundup® granules in saturated sucrose solution administered 2 h before testing	Spatial memory	Simple maze completion time-	24 h after exposure, times were lower than at 2 h, but still 5–8.5X longer than controls Simple maze course corrections—control bees 0, ED_{25} 1.3, ED_{50} 2.35	[60]
			Complex maze	Substantially and significantly after 24 h	
Zebrafish (*D. rerio*) 3-day larvae adults	Glyphosate Roundup® 96 h 0.01 mg/L 0.065 mg/L and 0.5 mg/L	Aversion avoidance memory	Dark/light association	Impaired by 0.5 mg/L Roundup®; other concentrations not significant Glyphosate alone not significant	[115]
Livebearer (*J. multidentata*)	Roundup® Original Roundup® Transorb Roundup® WG 96 h 0.5 mg/L	Long-term memory	Avoidance inhibition test	All fish spent more time in the light area in testing than training RWG: less time in light area in testing	[126]
Three–keeled pond turtle (*M. reevesii*)	Glyphosate ammonium eggs 2, 20, 200 or 2000 mg/L	Spatial learning	Maze	Longer time to cross maze; dose-dependent	[154]
Human	Accidental exposure	Parkinsonism	Mental exam	Short-term memory loss	[199]
Human	Occupational exposure		Benton visual retention test	Impaired visual memory	[191]
Human	Unknown exposure amount	Encephalopathy	Neuropsychological test	Day 2—memory problems Day 12—overall test score 22/30, 0/3 word recall, impaired memory and executive function 3 years—neuropsychological tests 28/30, $^{2}/_{3}$ word recall, improvements in memory and executive functioning	[197]

Table 12. *Cont.*

Animal	Exposure	Specific Learning/Memory Behavior	Behavior Test Used	Behavioral Outcomes	Source
Human	Commercial formulation Unknown amount	Hippocampal infarction	IQ and memory tests	At admission—memory normal Several hours—memory deficit, short-term memory loss, including of suicide attempt Day 9—short-term recall deficits 3 weeks—partial improvement; IQ = 70, verbal memory 52, general memory 64, delayed memory; 65 indicates retrograde and anterograde amnesia. 2 months—verbal memory 74, general memory 84, delayed memory 86 6 months—memory impairments remain.	[95]
Human	Chronic occupational exposure	Parkinsonism		No short-term memory loss	[75]
Human	Unknown amount	Encephalopathy		Short-term memory impairment, retrograde and anterograde amnesia	[198]

3.6. Social Behaviors

Studies on a variety of animal species have assessed the effects of pesticides and herbicides on social behavior. The scope of these investigations includes effects on anxiety-related and depressive-like behavior, aggression, autism spectrum disorders (ASD), and more (summarized in Table 13). In critical developing stages of the brain such as the prenatal, postnatal, and adolescent periods, exposure may be even more detrimental, having possible impacts not just on higher cognitive functioning like in learning and memory, but also on social and emotional behavior as well as the development of ASD [105,200]. Generally, herbicides like glyphosate have been reported to affect motor and emotional functioning in addition to sociability in several non-target animals. Though neurotoxicity of glyphosate on humans is less frequently studied, studies have made associations between glyphosate and neuropathology like ASD and Parkinson's disease.

Herbicides like glyphosate have been shown to cause neurotoxic effects linked to changes in mood such as anxiety-related and depressive-like behavior. In rodents, the open field (OF) test is commonly used to assess locomotor activity and emotional reactivity to new environments, where a tendency to stay in the peripheral areas in the OF arena, termed thigmotaxis, and thus, less time spent in the center, indicates anxiety-like behavior [107]. Elevated plus maze (EPM) tests have also similarly been used to assess anxiety in rodents. Employing these methods, studies on GBH exposure in mice have reported decreased locomotor activity [107,201], indicating effects on nervous system function, and increased anxiogenic behavior [105–107,202,203]. Ait Bali et al. [105,202,203] have shown that these effects are dose-dependent and occurred after subchronic (6 weeks) and chronic (12 weeks) GBH exposure, but not acute. Another study by Bicca et al. [204] assessed subchronic exposure of Zamba® GBH at 50 mg/kg on rodents and explored the potential therapeutic effects of the flavonoid, quercetin. The results showed increased anxiety in the EPM test with fewer open arm entries and less time spent in the open arm. These effects were largely recovered by quercetin. Conversely, some studies did not find anxiolytic behavioral effects of glyphosate in the OF test [193,201,205], and Joaquim et al. [201] noted reduced exploratory behavior of only male mice during the EPM test. Exposure to GBH during critical development stages of the brain may have important effects on emotional behavior later in life. De Castro Vieira Carneiro et al. [194] reported that mice between postnatal day (PND) 25–28 that were exposed to 0.3 mg/kg/day of GBH during gestation crossed lines more frequently in OF tests, suggesting hyperactivity, and exhibited increased marble burying behavior which may be indicative of anxiety. In another study, rats were exposed to either 0.65 or 1.3 g/L of GBH during gestation and lactation. Females at PND 45 that were exposed to the highest concentration of GBH crossed fewer squares in an OF test, indicating decreased locomotor activity. These effects were also observed in 90-day-old male and female rats exposed to either concentration of GBH. The authors state their findings are positively correlated to an increase in emotional response in adulthood [185].

Glyphosate also affects locomotor activity and anxiety in other non-target organisms such as zebrafish. A study assessing the potential effects of global warming on glyphosate toxicity found that zebrafish exposed to glyphosate at increasing temperatures spent more time at the bottom of the tank and had more erratic movements suggesting increased anxiety [206]. They also found that glyphosate exposure at increasing temperatures caused disruptions in the zebrafish's circadian rhythm, where they spent less time swimming during the light portion of the cycle and more in the dark portion. Ivantsova et al. [118] compared the effects of glyphosate and AMPA (glyphosate's main metabolite) as well as a mixture of the two on zebrafish larvae. While glyphosate, but not AMPA or the mixture, induced hyperactivity in zebrafish, there were no observed effects on anxiety with any of the treatments.

In livebearers, unlike what has generally been seen in rodents, unexposed fish spend more time in the peripheral areas in an OF test than the central area where there is increased predatory susceptibility, indicating natural anxiety behavior [126]. Two formulations of GBH, Roundup® Original and Roundup® Transorb, increased the amount of time fish spent in the central area, while a third formulation, Roundup® WG, did not. The authors suggest that this could be due to a depressive-like state coinciding with reduced alertness. Similarly, Lanzarin et al. [161] found that zebrafish embryos exposed to the highest tested concentration of GBH did not exhibit evasion behavior when introduced to an aversive stimulus compared to the unexposed embryos. This decreased perception of fear could be due to adverse effects on CNS development, specifically in the habenula region of the brain which plays a role in aversive response control.

While it is unclear whether the effects of GBH on evasion behavior are caused by a depressive-like state, other studies have also linked glyphosate exposure to depression-like behavior. Ait Bali et al. [105,202] reported that subchronic and chronic, but not acute, exposure to GBH not only induced anxiety in mice but also depressive behavior, where mice subjected to a tail suspension test and splash test showed a dose-dependent increase in immobility time and decrease in grooming time, respectively. These results were in agreement with Joaquim et al. [201], who also reported increased immobility in the tail suspension test with both male and female mice acutely exposed to GBH. Mice exposed to GBH also spent more time immobile in a forced swim test and this, like the anxiety effects previously discussed, also improved with quercetin therapy [204]. Rats exposed to 0.36% glyphosate in water from gestational day 5 until PND 60 demonstrated prolonged immobility time and decreased time climbing in a forced swim test, indicative of depressive-like behavior, though no effects on anhedonia-like behavior were seen [207].

Glyphosate affects honeybees' ability to carry out social activities that rely on functions such as directional flight [99], appetite [104], associative learning, and circadian rhythms [100]. Decreased social interaction was also observed in rodents exposed to GBH during gestation [183,208] and also throughout the lifespan from pregnancy until adulthood [193]. Impaired social behavior was also found in livebearers exposed to Roundup® for 96 h [126], as demonstrated by a preference for the side of the aquarium with fewer fish. De Oliviera et al. [183] found that maternal exposure to GBH reduced the number of ultrasonic vocalizations emitted by pups, which is an early social communicative deficit. Additionally, the pups exhibited increased latency to reach the GBH-treated dam's shavings, signifying a defect in olfactory discrimination which is important for social behavior development. In a three-chamber sociability test, GBH-treated mice spent less time and made less visits to another conspecific and spent more time with an inanimate object, indicating adverse effects on adult mice social skills [106]. While many studies have reported negative effects of GBH on social behavior, a few studies [161,194] did not identify such effects.

Changes in aggression also occur in some animals exposed to glyphosate. In Sanchez et al.'s [126] study, livebearers were tested for aggressive behavior by observing their proximity to their own reflection in a mirror, which indicated preference for an "opponent". All GBH-treated fish spent more time in proximity to the mirror and thus demonstrated more aggressiveness than non-treated fish. In contrast, Bridi et al. [115] reported that glyphosate impaired aggressive behavior in zebrafish, utilizing a similar methodology. Pinning behavior is an important assessment of play fighting behavior in rodents where the goal of the rat is to wrestle the opponent onto its back and stand over it [171]. Pinning behavior was impaired in both male and female offspring of dams exposed to the highest GBH dose of 150 mg/kg/day from day 15 of gestation to PND 7. Since pinning behavior is critical to the development of male rat sexual competence, this could affect sexual behavior in adulthood.

Over the past few decades, there has been a rapid increase in the prevalence of autism spectrum disorder (ASD), a neurodevelopmental disorder characterized by difficulties in social communication and unusually limited and repetitive behaviors and interests [209]. With the simultaneous increase in global herbicide and pesticide use, many studies assessing the association between pesticides and neurodevelopmental disorders like ASD have shown a strong relationship [200,210–212]. Del Castilo et al. [193] found that both male and female 3-month-old mice exposed to GBH since pregnancy exhibit more repetitive marble burying, a behavior used to assess stereotyped behavior in mouse models of autism. Other studies also support these findings [183,194], reporting an increase in repetitive/stereotyped behavior in rodents exposed to GBH during gestation and throughout the lifespan [193]. In addition, in a novel object recognition test, mice demonstrated cognitive deficits after maternal glyphosate exposure, suggesting ASD-like cognitive impairment [208].

Some case studies have assessed the effects of pesticides and herbicides on neurological disorders like ASD and Parkinson's disease in humans. For example, a study by von Ehrenstein et al. [79] examined birth data between 1998–2010 from the Central Valley of California, a major agricultural location. The risk of developing ASD correlates with exposure to glyphosate and other herbicides such as chlorpyrifos, diazinon, malathion, avermectin, and permethrin. This risk increases following prenatal exposure to ambient pesticides within 2000 m of their mother's residence during pregnancy. Exposure during the first year of life can further increase the risk of ASD with intellectual disability comorbidity. Other studies have linked glyphosate exposure, through occupational exposure or accidental ingestion, to Parkinsonian syndrome [75,199,213]. A case study by Zheng et al. [214] detailed the events of a previously healthy 58-year-old woman following acute glyphosate exposure, where the patient developed Parkinsonian syndrome that completely resolved after treatment with ATP, pralidoxime iodide, and scopolamine hydrobromide.

Social behavior is important to the procreation, survivability, and adaptability of species throughout the animal kingdom. In honeybees, for instance, social interaction and cooperation is vital to the survivability of the entire colony, as each member has specific tasks to carry out [215]. Social behavior in rodents also plays a role in the development of other cognitive and emotional processes which later form part of the adult behavioral repertoire [183]. Thus, disruptions in social behavior can have damaging effects to not just the individual organism but to whole populations, species, or ecosystems.

Table 13. Effects of GBHs on Social Behaviors.

Animal	Exposure	Specific Behavior	Behavior Test Used	Behavioral Outcomes	Source
Zebrafish (*D. rerio*)	Glyphosate and AMPA (0.1, 1, or 10 µM) or mix of both (1 µM) for 7 days	Locomotor activity and anxiety	Distance moved during alternating light and dark periods, Dark/light preference	Hyperactivity of zebrafish exposed to glyphosate but not AMPA or the mixture No effect on anxiety-like responses	[118]
Mice	Roundup® Transorb 25, 50, or 100 mg/kg;	Generalized behavior and anxiety	Open field, elevated plus maze, tail suspension	Decreased locomotion in female mice No effect on anxiety but reduced exploration in male mice Increased immobility time both males and females	[201]
Zebrafish (*D. rerio*)	Roundup® UltraMax 0, 1, 2 and 5 µg a.i./mL; 72 h	Escape-like response, anxiety/stress, social behavior	Visual stimulus response, nearest neighbor distance and inter-individual	Exposed larvae did not exhibit evasion behavior	[161]
Rat	ZappQI620 Syngenta; 50 mg/kg/day	Social behavior, ASD	Open field, social play behavior test, homing behavior test, hole board test	Reduced number of ultrasonic vocalizations in pups Decreased social interaction time in pups and deficit in olfactory discrimination Increased stereotyped behavior	[183]
Rat	Roundup® Transorb; 50 and 150 mg/kg	Play fighting behavior	Intruder play fighting test	Pinning behavior impaired in both male and females offspring	[171]
Zebrafish (*D. rerio*)	Glyphosate 1 ppm and 5 ppm for 96 h at 28.5, 29, 29.5, or 30 °C	Circadian rhythm and anxiety	Locomotor test, novel diving tank test	Disruptions in circadian rhythm Fish spent more time at the bottom of the tank with more erratic movements	[206]
Mice	GBH, unspecified formulation (0.039% *w*/*v*)	Social behavior, ASD	Three-chamber test, novel object recognition	Deficits in social interaction in offspring ASD-like cognitive impairment	[208]
Mice	Roundup®; lifelong exposure to low doses (0.075% *w*/*v*)	Social behavior	Open field, social approach test	Reduced time spent exploring the stranger mouse and increased repetitive behavior No effect on anxiety or locomotion	[193]
Mice	Glifloglex®; 2 mg/nostrils/day	Anxiety	Plus maze	Increased thigmotaxis and higher anxiety	[107]
Mice	Roundup® Original	depression	Forced swim test	Increased immobility time and decreased climbing activity	[207]

Table 13. *Cont.*

Animal	Exposure	Specific Behavior	Behavior Test Used	Behavioral Outcomes	Source
Livebearer (*J. multidentata*)	Roundup® Original, Roundup® Transorb, and Roundup® WG	Aggression, anxiety, social behavior	Open field, proximity to own reflection in a mirror	More time spent in proximity to the mirror More time spent in central area of open field	[126]
Mice	Glyphosate 0.3 mg/kg daily *per oral*	Anxiety, locomotor activity	Open field, social interaction, and marble-burying	More frequent crossing of lines in open field Increased marble burying behavior No effect on social behavior	[194]
Mice	Zamba® 50 mg/kg	Anxiety, depression	Elevated plus maze Forced swim test	Fewer open arm entries and less time spent in open arm Increased immobility time	[204]
Mice	Roundup® 500 mg/kg/day	Anxiety, depression	Open field, elevated plus maze, tail suspension, splash test	Increased anxiogenic and depressive behavior after subchronic and chronic exposure Dose-dependent increase in immobility time and decrease in grooming time	[105]
Mice	Roundup® 250 or 500 mg/kg/day	Anxiety, depression	Open field, elevated plus maze, tail suspension, splash test	Decreased time spent in center of open field after subchronic and chronic exposure Increased immobility time after chronic exposure Decreased grooming time after both subchronic and chronic exposure	[202]
Mice	Roundup® 250 or 500 mg/kg/day	Anxiety, social behavior	Three-chamber sociability test	More time spent with inanimate object Fewer visits made to conspecific	[106]
Mice	Roundup® 250 or 500 mg/kg/day	Anxiety	Open field, elevated plus maze	Increased anxiogenic and depressive behavior after subchronic and chronic exposure	[203]
Zebrafish (*D. rerio*)	Roundup® or glyphosate (0.01, 0.065, and 0.5 mg/L	Aggression	Proximity to own reflection in a mirror	Reduced time spent in proximity to the mirror Decreased number of entries into the mirror contact zone	[115]
Human	Acute glyphosate exposure	Parkinsonism		Parkinsonism syndrome that resolved after treatment	[214]
Human	Ambient pesticides including glyphosate	ASD		Increased risk for ASD after prenatal exposure Increased risk for ASD with comorbid intellectual disability after exposure during infancy	[79]

4. Discussion

Glyphosate-based herbicides impact a wide variety of behaviors among animals, including activity, foraging and feeding, anti-predator behavior, courtship, mating, maternal behavior, learning, memory, anxiety-like behavior, depression-like behavior, aggression, and other social behaviors. When given the opportunity, many types of animals are able to detect GBH contamination. They avoid areas contaminated with GBH when possible (e.g., fish [121,129]). In addition, animals sometimes eat less when the food itself is contaminated with GBH. Food containing GBH led to some species decreasing food consumption [134–136], while in others, it had no effect [144]. For example, bees showed different results in different studies, even though they had similar modes of exposure. Bees increased consumption of GBH-contaminated food [140], decreased food consumption [138,139], or their food consumption was not affected by glyphosate contamination [104,141–143]. It appears that the variation could be caused by season, which may affect honeybees' willingness to feed [140,216]. It could also be due to the differences in the herbicide formulation used, and dosage, as each formulation contains different in ingredients in addition to glyphosate. The decrease in food consumption sometimes seen may be due to GBHs affecting the taste or smell of the food, thereby either disrupting food recognition or overcoming the recognition of food with a stronger aversive cue. Taken together, these provide evidence of the ability of at least some animals in some situations to detect and avoid GBH contamination. However, there is some concern that co-exposure to different pollutants may confuse animals' abilities to perceive, identify, and/or avoid individual toxins, and specifically, that glyphosate can mask identification of other agrochemicals [217].

GBH exposure affects many different animal species by changing their level of activity. Many studies indicate that glyphosate reduces activity, including overall activity levels, speed, distance traveled, coordination, and navigation efficiency. GBH-induced activity reduction affects terrestrial animals across taxa (see Table 5), regardless of the mode of activity (walking, crawling, flying), age or stage of animals (e.g., [115,116]), or method of GBH administration [112]. However, in aquatic animals like fish, GBH exposure can increase or decrease activity depending on concentration, duration of exposure, and distribution of the contaminant within the body of water. Increases in activity might allow animals to swim away from contaminated water, while decreases in activity might reflect a more general or long-term response to GBH exposure. Decreased activity would likely affect many other aspects of animals' lives, including foraging and feeding, anti-predatory behavior, courtship, mating, and other social behaviors, ultimately impacting both the survival and reproductive aspects of fitness for exposed animals. When GBH contamination is widespread at high enough concentrations, species and ecosystems become threatened.

Pre-exposure to GBH for different durations affects foraging and feeding behavior. In most studies, animals decreased the amount of uncontaminated food consumed or increased the time to forage or feed on uncontaminated food after pre-exposure [145,146,153,154]. However, increases in food consumption after GBH exposure were also documented [147–149], while other studies showed that pre-exposure had no effect on feeding behavior [152,155,156]. Some predators (primarily wolf spiders) became hyperactive after exposure to GBH but less coordinated, improving their catches per minute but increasing the number of lunges required for each catch [149,150]. Impacts of GBH on foraging and feeding behavior will result in negative consequences for exposed organisms if they expend too much energy foraging or acquire too little food, particularly if the result is that they are unable to maintain sufficient energy and nutrients to maintain normal functions, including reproduction.

Exposure to GBH affected many prey species' anti-predator capabilities. Zebrafish pre-exposed to GBH return to and spend more time in areas which had a predatory stimulus, indicating loss of predator awareness and putting them more at risk of predation. Zebrafish naturally spend time in peripheral areas, suggesting that they are risk-aversive, which can make them less susceptible to predation, but GBH exposure impaired their ability to detect danger and apparently decreased their baseline level of fear [157–161]. Other species displayed an increase in activity after pre-exposure to GBH and brief exposure to predator cues [162,165], making them more prone to predation. Meanwhile, in other species a decrease in activity was recorded in the presence of predators and predator cues after exposure to GBH [166,167]. GBH exposure impaired some species physically, decreasing escape speed after exposure [127,147]. Furthermore, in a few studies, no effect from pre-exposure to GBH on anti-predator behavior were recorded [130,167]. Deactivation or masking of predator cues by GBHs was documented [162,163], similar to GBHs masking the presence of other agrotoxins, as mentioned above [217]. Since some organisms rely on olfactory detection of predator cues in their environment; cues deactivated or masked by GBHs may increase vulnerability. In essence, the evidence suggests that exposure to GBH disrupts some animals' anti-predator capabilities, making them vulnerable to predation with potential repercussions for food webs and ecosystems.

Glyphosate and GBHs can act as endocrine disruptors and negatively impact the reproductive systems of animals. Exposure to glyphosate has been linked to reduced courtship, mating, and fertility rates, as well as impaired maternal behavior in animals. Studies have found that exposure to glyphosate can lead to difficulty conceiving in mice and decreased fecundity and fertility rates in different species of fish, invertebrates, and rodents [38,61,146,168,170,178–182,184,186,195]. GBH exposure has also been linked to diminished pinning behavior in rodents, decreased female sexual behavior, and disrupted aromatase activity, leading to the impairment of sexual behavior in female offspring [171]. Exposure to glyphosate has been found to decrease masculinization of male rodents exposed before puberty and impaired sexual chemical communication between female and male wolf spiders, reducing the male spider's ability to find their mate [169,172–175].

Chronic sublethal exposure to glyphosate and another pesticide, thiacloprid, negatively affected colonies of ants, decreasing the number of eggs and pupae and resulting in smaller colonies [177]. While some studies have found no adverse effects in terms of the impact of GBH on courtship, fertility rates, and maternal behavior [129,152,176,183,185,187], it is important to note that the effects of glyphosate and GBHs on reproductive behavior can vary depending on the species, the level of exposure, and the stage of reproduction. Overall, these studies suggest that exposure to glyphosate can lead to disruptions in maternal behavior, courtship, and fertility which can have negative impacts on the development and survival of offspring.

Researchers working with bees, rats and mice, and other animals have extensively explored the effects of GBH on a variety of types of learning and memory. While there are some mixed results, taken together, these studies suggest that GBH exposure reduces spatial and some types of sensory learning. Memory of all types discussed are impaired by GBH exposure, whether exposure occurs before learning or between learning and recall ([189]; human studies). Spatial learning [60,99,192] and memory [60,154,192,195] are both impaired by GBH exposure, potentially interfering with the ability of animals to navigate effectively in their environment. For example, exposure impairs cognitive abilities needed to integrate spatial information to successfully return to the hive [99]. GBH exposure interferes with some types of sensory learning [98,104,138,188–190] and all types of sensory memory studied [98,104,189,190], which could impact foraging, recognition of food, recognition of mates, recognition of offspring, and other social interactions. Other types of memory harmed by GBH exposure include recognition memory and aversive stimulus memory [106,107,115,126,192,195,196]. In addition, case studies and population assessments indicate that GBH exposure, both incidental and through ingestion, impairs various types of memory in humans, especially visual memory [191], word recall [95,197], and short-term memory [95,198,199], while in some cases, it induces both anterograde and retrograde amnesia [95,198]. In terms of both learning and memory, more difficult tasks seem to be more affected by exposure than simple ones [60,189].

The effects of glyphosate and GBH on anxiety-like behavior and social behavior, in addition to the development of neurological disorders, have been demonstrated throughout the literature. Most commonly, GBH exposure causes increased anxiety [105–107,202–204] and changes in motor activity, whether animals exhibit decreased locomotion [107,201] or hyperactivity [118,194,206]. GBHs also cause depressive-like behavior [105,201,202,204,207], changes in aggressiveness [115,126], and ASD-like cognitive impairment [183,193,208]. Social behavior is also affected by GBH exposure, as demonstrated by deficits in early communication and olfactory discrimination [183], impairment of functions needed to carry out social activities [37,99,100,104], and decreased social interaction with other animals of the same species [106,126,183,193,208]. Interestingly, impaired evasion behavior was seen in multiple aquatic systems, demonstrated by an increased time spent in the central areas of the tank [126,161]. Of the studies assessed here, however, rodents generally exhibit the opposite behavior, spending more time in the periphery of an open field arena. This suggests that responses to GBH may be species and/or habitat-specific. In addition, epidemiological studies report adolescent-related psychiatric illness and sensorimotor deficits resulting from GBH exposure [105]. Other studies in humans have demonstrated a relationship between glyphosate and neurological disorders such as ASD [79,200,210,211] and Parkinsonism [75,199,213,214].

While there is variation among the reported results, some of these could be attributed to differences in methodology, especially age of exposure, duration of exposure, dose or concentration, and GBH formulations. For example, prolonged exposures cause more toxic effects and more severe effects than acute exposure [105,201,202]. The dose of GBH fed to honeybees may have led to variation in amount of feeding behavior [104,138–143]. Similarly, Gallegos [185] and de Oliveira [183] observed no adverse effects of GBH exposure on maternal behavior, which may be attributed to lower doses and different formulations of GBH than in other similar studies. Griesinger [174] and Ward [176] used different concentrations and different formulations of GBH, which may be the cause of their conflicting results about courtship behavior. No effect of glyphosate on associative learning was found when a very low dose was administered [190], while other studies used higher concentrations and identified learning deficits [98,104]. A study that did not observe effects on either anxiety or novel object recognition used lower doses of glyphosate than in other studies [193].

While it is important for researchers to use ecologically relevant doses, any concentration up to the recommended dose for application is ecologically relevant in some situations, such as brief exposures when an animal is in an agricultural field or other area while it is being sprayed, or eating nectar, pollen, or other parts from a plant that was recently sprayed. A great deal of variability in experimental approaches, including concentration, duration, method and medium of exposure, etc., make generalizations difficult. However, the methods used in most lab and field studies seem to use exposures that are between concentrations as applied and those measured in different environments at times mostly unspecified with regard to local or nearby spraying (compare Table 1 to Tables 5–13).

Commercial formulations of GBH include a variety of adjuvants and other ingredients that are often listed as proprietary information and therefore are not disclosed on packaging. These additives could have synergistic effects, making it difficult to attribute toxicity to any one specific ingredient, and this could contribute to the differences between formulations. Bridi [115] found that Roundup® exposure affected memory more than exposure to glyphosate alone, and Sanchez et al. [126] compared two different Roundup® formulations with somewhat different results. Another study found that Roundup® had more of a negative impact on anti-predator capabilities and an increase in food consumption compared to glyphosate [147]. Zebrafish embryos exposed to Roundup® and glyphosate had contrasting effects—Roundup® induced more swimming and glyphosate had the opposite effect [119].

4.1. Mechanisms of GBH-Induced Behavioral Impairments

Glyphosate can act via a variety of mechanisms, both in general and as it relates to behavioral toxicity. Two of these mechanisms, oxidative stress and disruption of the gut microbiome, are general, disrupt the function of a variety of organs throughout the body, and have widespread effects on many aspects of physiology and behavior. Other mechanisms that specifically cause behavioral responses to GBH exposure involve endocrine and neurological control of these behaviors.

Exposure to glyphosate increases reactive oxygen species and causes inflammation, both of which affect learning and memory. Increases in anti-oxidant enzymes SOD and PO correlate with learning and memory impairments in mice [195], and is associated with synaptic plasticity for short-term and long-term memory storage [106]. Recognition memory impairment is related to other markers of antioxidant stress, including MDA content, CAT activity, and GPx activity in rats [196]. GBH-induced memory loss in humans has also been attributed to oxidative stress [198]. Oxidative stress can also lead to inflammation, which can cause morphological changes. Several proteins associated with inflammation increase in concentration in the hippocampus and prefrontal cortex after exposure to GBHs, specifically GFAP and Iba-1, and of TNF-alpha in the hippocampus only [106]. Oxidative stress has also been proposed as a mechanism of glyphosate-induced toxicity with regard to avoidance behavior, [114], reproductive behaviors [114,183], and anxiety and depression [204,207].

Several studies have reported that glyphosate disrupts the normal gut microbiota, promoting overgrowth of pathogenic bacteria [55,105,202,218,219], which could have dangerous impacts on the organisms' health in general. Because mammal gut microbiota utilize the shikimate pathway to synthesize precursors to neurotransmitters like serotonin and dopamine [219–221], disruption of this pathway by glyphosate could also have important neurologic health implications, including causing anxiety and depression-like behavior in mice [202].

Glyphosate as an endocrine modulator has been suggested as a potential mechanism of toxicity, particularly regarding reproductive outcomes, including courtship, mating behavior and maternal behaviors. Glyphosate inhibition of aromatase, the enzyme responsible for the irreversible conversion of androgens to estrogen, causes an imbalance between androgens and estrogens. Particularly during the neonatal period in rats, this disruption in steroid sex hormones could interfere with brain development of the sexual organization and thus impair sexual behavior in adulthood [106,171]. Male rats who were exposed to glyphosate showed higher levels of testosterone and estradiol compared to the control group. The higher levels of testosterone levels could explain why the male's sexual partner preference increased dramatically towards the females [172]. Exposure to the herbicide GLY-BH decreased specific binding to D1-DA receptors in the nucleus accumbens, basal extracellular dopamine levels, and high-potassium-induced dopamine release in the striatum. This resulted in hypoactivity and impaired maternal behavior, possibly due to blockage of the Ait-Balistriatal and mesolimbic systems. The decrease in maternal grooming behavior may be a result of perinatal exposure to the herbicide, as it has been shown that decreased grooming behavior is associated with decreased D1 receptor activation [184].

Neurological mechanisms of glyphosate toxicity that contribute to impairments in learning, memory, anxiety, and other social behaviors include structural localization, neurotransmitter activity, and oxidative stress and inflammation specifically within the brain. The two most important structures related to learning and memory and implicated in GBH toxicity are the hippocampus and the prefrontal cortex. GBH toxicity to the prefrontal cortex may be morphogenic, related to the expression of brain-derived neurotrophic factor and tyrosine-related kinase receptor [106,195]. In rats, hippocampus involvement is related to decreased dendritic complexity, synaptic spine formation and maturation, and therefore decreased formation of synaptic terminals [192]. Hippocampal lesions were also associated with learning and memory loss in mice [106]. In humans, hippocampal lesions after GBH poisoning [95,197,198] resolved after several months [95,197].

One cause of GBH induced neurotoxicity to the hippocampus, PFC, and striatum is that glyphosate mimics glycine, a required cofactor for glutamate activation of NMDA. According to this mechanism, glyphosate hyper-excites NMDA glutamate receptors, causing cell death [196–199]. In bees, glyphosate binds to NMDA receptors more efficiently than endogenous glycine, making GBHs more toxic to bees than to humans [60]. Another neurotransmitter involved in glyphosate toxicity is acetylcholine. Specifically, GBHs interfere with acetylcholine esterase activity, reducing its concentration in the hippocampus, prefrontal cortex and striatum [106,195,196].

Potential mechanisms of glyphosate neurotoxicity related to depression and anxiety have also been extensively discussed. Sulukan et al. [206] suggested a possible mechanism involving an important receptor for serotonin, 5-HT4R, which modulates depression and anxiety responses. Some studies have discussed changes to the dopaminergic, seritonergic, and glutaminergic systems as possible explanations for anxiety and depressive-like behavior [105,161,183,185]. Influences on brain development, sexual and play behavior in rodents could be associated with glyphosate as an endocrine modulator, since glyphosate inhibits aromatase, the enzyme responsible for the irreversible conversion of androgens to estrogen [171]. Other mechanisms have been explored, such as inflammatory cellular disorganization [106], disruption of manganese homeostasis [219], changes in gene expression [118,203], and oxidative stress [204]. In conclusion, more research is warranted to elucidate the mechanism by which glyphosate causes neurotoxicity in non-target animals.

4.2. Further Research

Many behavioral areas have been researched in only a few taxa (Figure 1), often common model systems. None of the articles we were able to identify studied behavioral effects in mammals other than mice, rats, humans, and birds, and only a few used amphibian or reptile systems. While human behavior was examined in terms of effects of GBH on memory, there were no studies of how other human behaviors are affected by GBHs. Even among invertebrate models, honeybees were disproportionately the focus of the studies reviewed here. While honeybees serve a critically important role in pollination, so that their behavior might be disproportionately important, and their exposure disproportionately likely, for example in agriculture, other insects and non-insect invertebrates should also be studied in terms of the effects of GBH on behavior. Overall, future studies are needed to address the effect of glyphosate and GBH on behavior in a wider range of taxa, including mammals other than mice and rats.

Additionally, studies have been conducted on animals in a laboratory setting. More research is needed to understand the full extent of glyphosate's impact on activity, foraging, anti-predatory behavior, and reproductive behaviors in organisms that are exposed to GBH in natural settings. Field-based studies should focus on exposure at environmentally relevant doses, ranging from those applied in agricultural settings to smaller concentrations that would persist in areas affected by agricultural overspray, drift, or runoff. These field-based studies are critical to better understand the impact of GBHs on the behavior of animals in their environments, and by extension the overall impacts of GBH exposure on ecosystems and ecosystem services.

More research is also needed on mechanisms of behavioral changes, tying together physiological results with consequential behaviors. While research on physiological toxicity is extensive, the relationship between these physiological effects and behaviors are only partially understood. Given that experimental research on humans is nearly impossible, fully delineating the mechanisms of behavioral GBH toxicity in animals can help us understand which specific behavioral results from animal experiments are likely to also apply to human behaviors, and ultimately the potential impacts on human populations and human wellbeing.

5. Conclusions

Glyphosate, the active ingredient in many herbicides, has been the subject of much debate due to its potential toxic effects on non-target organisms. In this review, we examined the effects of glyphosate and GBHs on animal behavior. While there are some discrepancies between the methodologies and results, studies demonstrate that glyphosate impairs activity, foraging and feeding, anti-predator behavior, reproductive and maternal behaviors, learning and memory, and social behaviors in animals. Although glyphosate toxicity in non-target organisms has been studied, its mechanisms and effects on human health are still unclear, justifying further research and investigation. Due to the possible dangers and unknown impact of glyphosate in humans and on the environment, we advise caution when using glyphosate and GBHs and suggest implementation of alternative agricultural and municipal practices.

Overall, animal behavior endpoints should be considered in regulatory decisions about chemical environmental contaminants. Appropriate performance of many types of behavior impact reproduction and survival, food webs, and therefore, ecosystem health [95]. Behavior, as a sub-lethal endpoint, provides a particularly sensitive test for biotic disruptions that result from environmental contamination with chemical pollutants, and importantly, provides more accurate assessment of the effect of contaminants on real-world ecosystem health than mortality-based endpoints alone [222]. For example, the sensitivity of behavioral endpoints are 10 to 1000 times greater than those for mortality at accurately providing an early warning about chemical contaminants. [223]. Other benefits of examining animal behavior in ecotoxicological assessment include that it is often inexpensive, non-invasive, and increasingly can be automated [96,223]. In fact, a variety of new tools and technologies, reviewed in [222], allow for behavioral investigation of the effects of contaminants with higher resolution and at larger scales, further increasing the usefulness of behavioral outcomes for making regulatory decisions. Including animal behavior in regulatory decisions would therefore allow a more complete and accurate understanding of the impacts of new and emerging contaminants, low concentrations of contaminants, and allow identification of contaminants of concern much more quickly than waiting for more widespread indications of ecosystem collapse, perhaps after it is too late.

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