

Review

# Bird Welfare in Zoos and Aquariums: General Insights across Industries

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**Abstract:** Animal welfare is a priority across accredited zoological institutions; however, historically, research has been prioritized for mammals. Bird-focused studies accounted for less than 10% of welfare research in zoos and aquariums over the last ten years. Due to the lack of scientific publications on bird welfare, zoo scientists and animal practitioners can look to other industries such as agriculture, laboratories, and companion animal research for insight. This qualitative review highlights findings across industries to inform animal care staff and scientists on the welfare needs of birds within zoos and aquariums. Specifically, the review includes an overview of research on different topics and a summary of key findings across nine resources that affect bird welfare. We also highlight areas where additional research is necessary. Future welfare research in zoos and aquariums should prioritize studies that consider a diversity of bird species across topics and work to identify animal-based measures with empirical evidence. Moving forward, research from other industries can help develop innovative research on bird welfare within zoos and aquariums.

**Keywords:** bird habitats; substrate; flooring; lighting; sound environment; environmental enrichment; social management; human-animal interactions; genetics; nutrition



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## 1. Introduction

Animal welfare is a top priority for accredited zoos and aquariums [1,2]. However, animal welfare research remains biased toward mammalian species within zoological facilities [2–5]. Over the last ten years, bird-focused studies have accounted for less than 10% of all welfare research in zoos and aquariums, with greater rheas (*Rhea americana*) and greater flamingos (*Phoenicopterus roseus*) being the most commonly studied bird species [6]. We must address the lack of research since significantly more birds are housed in zoos and aquariums than mammals [5]. An across-industry evaluation can further progress and benefit the welfare of birds within zoological organizations. Such an evaluation can uncover techniques typically used in laboratory, farm, and companion animal studies and expose scientists to different perspectives, methodologies, and subject matters [7]. Thus, the current review will broadly investigate how resource-based measures, also referred to as inputs or environmental variables, impact bird welfare across industries and relate those findings to zoo and aquarium-housed birds. Most of the information in this review derives from the agricultural sector since most bird welfare research is on farmed chickens. The review is separated into sections on housing, substrate and flooring, lighting, sound environment, environmental enrichment, social management, human–animal interactions and relationships, genetics, nutrition, welfare assessments, and future directions.

Welfare assessment typically falls into three categories described by Fraser et al. [8]: basic health and functioning, affective states, or natural living [9]. In zoos and aquariums, research focuses heavily on assessing bird welfare through “natural living” or the expression of natural behavior at the individual level. Zoos and aquariums have evolved from using negatively biased assessments such as the Five Freedoms to positively frame

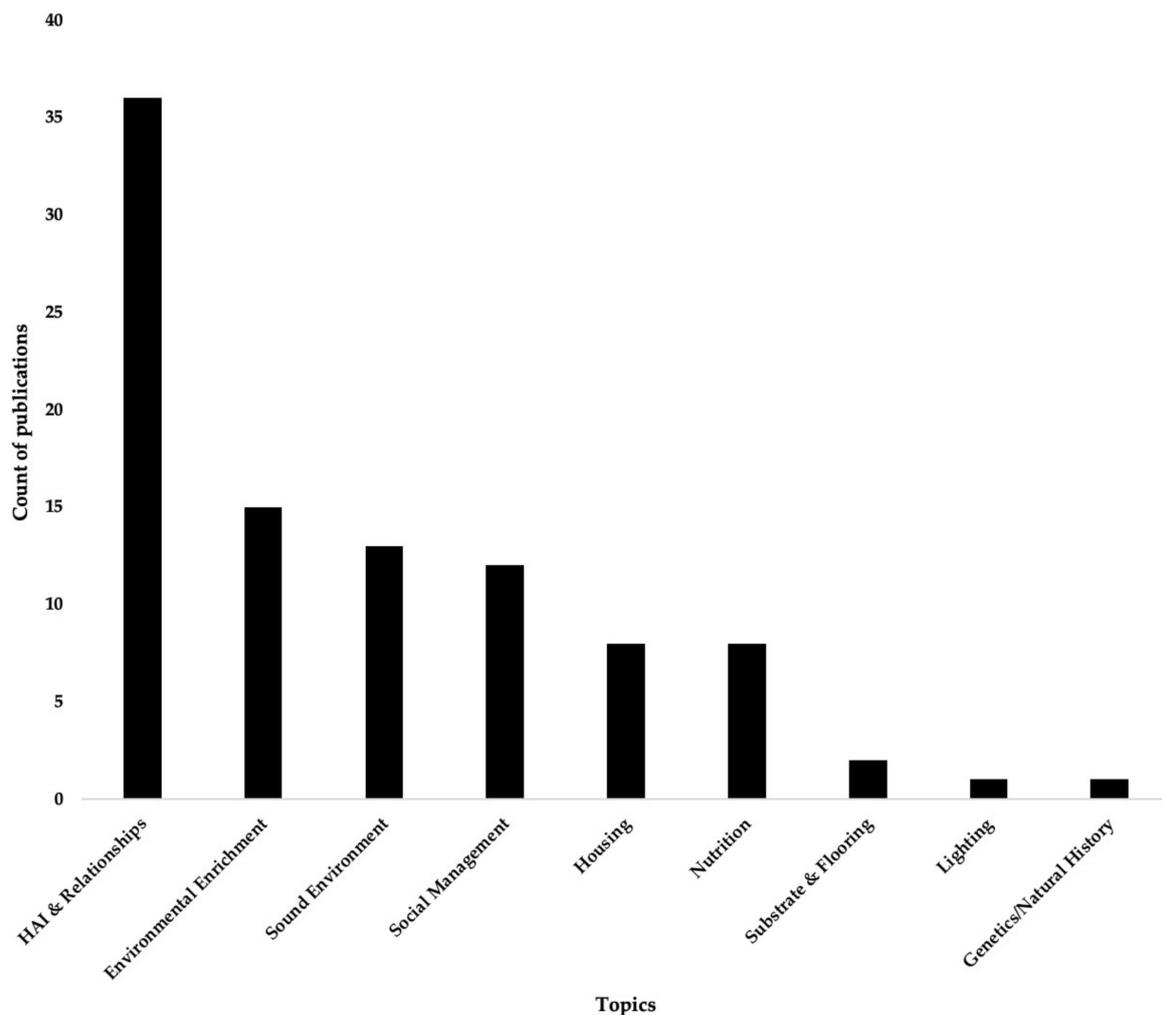
evaluations such as the Opportunities to Thrive or the Five Domains Model to assess the quality of natural living in animals [2,10]. Frameworks such as this enable scientists and animal care staff at zoos and aquariums to discover shortfalls that were not obvious under previous evaluations. For example, when assessing housing, birds are provided the opportunity to “self-maintain” and “express species-specific behaviors” with the inclusion of natural shelters, free-flight aviaries, and dynamic perching instead of simply being “free of discomfort” [11]. Outside the zoological industry, it is generally more common to investigate bird welfare at the group level. For example, a group-level study could investigate how different housing impacts bird welfare by assessing disease prevalence or the pervasiveness of injury across the flock, many times postmortem [12–14]. Group-level measures such as this could be advantageous for monitoring the welfare of larger flocks within zoos and aquariums. Across all industries, it is least common to assess bird welfare through emotional or affective states, which are defined as subjective states usually characterized as positive or negative and vary by arousal levels [9,15]. Examples of such states are excitement, pain, frustration, and pleasure [9]. The lack of this evaluation is most likely due to the complicated nature of understanding nonhuman emotions [16]. Considering affective states should not be overlooked as they are an essential part of a holistic welfare assessment.

We designed this manuscript as a qualitative conceptual review of the current state of bird welfare research by drawing from outside industries in conjunction with zoos and aquariums. Each section is purposely broad (rather than species-specific) to illustrate similarities and differences across industries. Priority areas with the greatest research need are addressed within each section and revisited in the Section 12. The broad nature of this review makes it particularly useful for early career researchers and animal care staff with limited knowledge of bird welfare. However, established individuals in animal care and research can also benefit from the concepts introduced, which are uncommon in zoo bird welfare. This is the first review compiling information on bird welfare across industries to be applied within zoos and aquariums. Our goal of creating a broad review as a reference for bird welfare across taxonomic groups should not overshadow the essential need for future research on species-specific guidelines for birds.

We qualitatively selected articles by searching Google Scholar, Web of Science, and ScienceDirect to account for all relevant bird welfare articles. Search terms were intentionally broad and included zoo + bird welfare, zoo + avian welfare, farm + bird welfare, farm + avian welfare, companion + bird welfare, companion + avian welfare, laboratory + bird welfare, and laboratory + avian welfare. The initial search resulted in 3619 publications. Sources were required to have been peer-reviewed articles, review papers, or dissertations published in English to maintain a manageable scope. Additionally, articles not containing the word “welfare”, “well being”, or “wellbeing” within the title, abstract, keywords, or full text were eliminated. We acknowledge that some of the articles eliminated under these criteria could have improved animal welfare in zoos and aquariums. However, since the stated or implied goal was not welfare-based, we removed them from the search, similar to other recent reviews [6,17]. In some cases, articles that did not meet the listed criteria were included because they provided supplementary information on topics with a scarcity of published work or illustrated examples of concepts. The reference section includes the final sources.

Figure 1 describes the count of bird welfare publications conducted in zoos and aquariums from 1997 to 2021. The final literature search was conducted on 2 January 2022, to ensure all publications from 2021 were accounted for. A single study could fall into one category or span multiple topic areas. Four studies that assessed zoo bird welfare were excluded from the graph below because they focused on inputs or resource-based measures that we did not break into distinct sections (e.g., evaluating new measures, emotional states, etc.). Reviews were also excluded. Overall, bird welfare research in zoos and aquariums is lacking, with only 96 publications that fit our criteria discovered over 24 years. Studies that consider the influence of human presence, interaction, manipulation, or relationships (seen

as “HAI & Relationships”) are most prevalent, followed by those that study the impact of environmental enrichment and sound on bird welfare. Although enrichment was one of the more commonly studied topics here, a recent review found that only about 8% of all experimental enrichment research focuses on birds, with domestic chickens, *Gallus gallus domesticus*, accounting for the vast majority of these studies [18]. Even the areas of greatest interest in bird welfare have significant disparities compared to other taxonomies. The current review will utilize findings across industries to gain insight into zoo and aquarium bird welfare and highlight areas of greatest need for future research and husbandry.



**Figure 1.** Count of bird welfare publications conducted in zoos and aquariums arranged by topic (1997–2021). A single study could fall into one category or span multiple topic areas ( $N = 96$ ).

## 2. Housing

Habitat design for birds varies greatly across zoological institutions and is understudied [19]. The habitats of companion birds can be equally variable since the owner decides the design, and it can be challenging to sample households [20]. Quite the opposite is the agricultural sector, which typically has a uniform environment with the ideals of optimal and efficient production, which creates the opportunity for large-scale, multi-farm studies [14]. A key concern of proper housing for birds across all industries is the ability to display natural behaviors. In exotic species, it is common to compare the behavior of animals under human care to their wild counterparts as a measure of welfare [21]. If an environment allows an animal to engage in all the behaviors it would in a natural setting, then it is assumed that most of their needs are met [22]. Stereotypic behavior in the form of route-tracing, feather damaging behavior, and oral fixations are linked to sub-optimal

housing conditions and behavioral restriction, which can alter behavioral control, cognitive processes, and health [23–25]. An awareness of laboratory and agriculture research on compromised welfare states in response to housing will enable zoo and aquarium professionals to identify variables that contribute to negative welfare and ensure the environments of birds under their care are designed accordingly.

An abundance of field behavior data can act as a baseline to assess the welfare of some bird species in smaller zoo populations [26,27]. Similarly, the expression of natural behaviors such as preening, dustbathing, nesting, and locomotion are used to signify positive welfare states of poultry [28,29]. Birds typically perform these behaviors when they are comfortable with no perceived threats and possibly experience reduced stress and contentment when doing so [16,30]. The inability to display internally motivated behaviors, such as nesting in hens and swimming in ducks, can result in frustration leading to compromised welfare [31,32]. Additionally, enclosures that allow arboreal bird species to fly are thought to be optimal for bird welfare [33]. In habitats where flight is restricted due to safety concerns, birds are commonly deflighted via pinioning (amputation of the wing tip) or wing clipping (regularly clipping flight feathers). Both procedures are speculated to impact welfare negatively [34,35]. Pinioning is highly controversial, such that some countries have outlawed the procedure entirely, and organizations of health and welfare such as the American Association of Avian Veterinarians (AAV) have publicly denounced its application [36,37]. Even with such a controversial topic, research is limited and difficult to generalize [34,35]. A recent study that spanned twenty-one German zoos compared the adrenal activity and behavior of great white pelicans (*Pelecanus onocrotalus*) that were either deflighted (via pinioning), wing clipped, or non-flight restricted found no significant differences in corticosterone levels in the feathers of deflighted or non-restricted birds. However, wing clipped birds had higher corticosterone levels when compared to both groups, indicating that wing clipped birds may be experiencing chronic stress due to repeated capture for the procedure [38]. Alternatively, a study that compared different forms of flight restraint (including no restraint as a control) on corticosterone and the behavior of greater flamingos across twelve zoos found no significant difference between the control and flight-restricted birds [39]. It is worth noting that the focus of most deflighting research is on zoo-housed species that naturally spend much of their lives on the ground or in the water with their only purpose for flight being to flee predators or migrate [36]. Understanding the motivation behind migration is extremely difficult since birds may still be innately driven to migrate even with optimal food, housing, and welfare standards [40]. Future research should focus on how deflighting impacts the welfare of birds with long travel distances.

Indoor enclosures without outdoor access are typical in zoos and aquariums. In such environments, egg-laying hens display more natural behaviors, have increased activity, reduced fearfulness, and improved bone strength compared to caged systems [41]. However, this form of housing in poultry sometimes results in increased aggression and a higher prevalence of lesions since birds are typically in very close proximity with their conspecifics [42,43]. In zoos, invasive human interventions such as flight restriction of arboreal species are reduced in indoor free-flight housing systems since flight is limited by physical barriers [44]. Two studies on Humboldt penguins (*Spheniscus humboldti*) in indoor enclosures have begun to pave the way for future exhibit and husbandry research by evaluating specific aspects of design across institutions such as exhibit size, details of water sources (size, water type, and filtration system), water/land ratio, and level of disturbance from visitors [19,45]. Both studies found that various habitat-related variables, such as nest box and flooring substrate, use of chlorine, and total enclosure size, including pool and land areas, influenced penguin breeding and concluded the need for further research to optimize exhibits for this species.

When given outdoor access, chickens increase their behavioral repertoire with more time spent active, investigating, dustbathing, and preening [32,46]. Outdoor access also reduces injuries and health conditions related to prolonged inactivity and decreases fear-

fulness [43,47,48]. Indoor housing with outdoor access allows birds to interact with conspecifics, which improves welfare through sociality, but also creates an opportunity for increased aggression, sometimes resulting in poorer feather condition [43,47,49]. Conversely, studies have demonstrated that poultry with outdoor access have no significant difference in feather condition compared to other systems [50,51]. In some cases, better feather condition was correlated with increased use of the outdoor space [52]. Similarly, it is thought that housing with outdoor access decreases growth and increases mortality rates [53]. However, several studies have disputed these claims with similar or better survivability and growth rates when allowing outdoor access [30,50,54]. Outdoor access in agriculture can improve air quality, which can be very poor in closed systems due to lacking ventilation and dust from litter [55]. Research on outdoor ranging behavior in broiler chickens found that the more frequent and the further the distance animals ranged from the home shed was correlated with improved welfare [48]. Poultry range use can be impacted by time of day, seasonality and climate, and if protection from weather elements (e.g., provision of shade in the summer and indoor access in the winter) is provided [56]. Predation of poultry has been reported as an issue at some farms that provide outdoor access and should be considered when designing habitats for zoo birds [57]. To design optimal outdoor spaces for zoo birds, we can reference natural history information in combination with research on poultry ranging behavior. Improvements associated with outdoor access in poultry, such as increased activity levels, behavioral repertoires, and survivability, are encouraging for birds across industries.

Overall, housing encompasses many variables that can impact bird welfare in zoos and aquariums. Even with in-depth studies as presented above, a system for optimal welfare is difficult to determine and greatly depends on how welfare is defined and the study species [43,47]. Research on housing is commonly biased toward anthropogenic views of conditions animals need to thrive, often lacking empirical evidence [3]. Conflicting results are likely due to variability across institutions, which creates an inability to test variables independently, with many characteristics contributing to study findings. Zoos and aquariums can benefit from considering research in the agricultural sector; specifically, the influence of outdoor access on bird welfare and precautions to take when managing species indoors. However, when referencing poultry literature to aid in the design and management of zoo bird habitats, we must account for the lack of domestication in exotic species and the need to tailor the habitat to each individual bird.

### 3. Substrate and Flooring

Inadequate flooring and generally sedentary lifestyles can cause foot conditions such as bumblefoot (pododermatitis, plantar lesions) and footpad dermatitis, which, untreated, can lead to lameness, behavior changes, and even death [58–61]. In zoo and aquarium-raised penguins, the presence of bumblefoot is significantly correlated with sex, weight, activity levels, and substrate [62,63]. It is recommended to replace smooth surfaces with variable, textured ones since penguins that spend more time on smooth concrete develop more lesions than on grated surfaces [62]. Poultry housed in non-cage systems typically have deep litter (wood shavings or straw material) as flooring, which encourages physical activity through the display of natural behaviors such as dust bathing, scratching, and foraging [64]. The provision of litter for zoo and aquarium birds is not standard, but the increase in behavioral repertoires seen in poultry may make litter worth considering for terrestrial birds [62]. However, if litter is implemented in zoos and aquariums, it should be used with caution since irregular maintenance contributes to significant welfare concerns in poultry [65]. For example, if the litter is too dry, it causes respiratory problems, and overly moist litter is the leading cause of footpad dermatitis and hock burn in poultry, two of the most common health indicators of poor welfare [66,67]. In indoor poultry enclosures, it can be challenging to tease apart the interchangeable impact of substrate quality and stocking density since these facilities allow for more birds, creating more waste and inadequate quality substrate. However, when evaluating environmental welfare risk factors in a

large-scale farm study (2.7 million birds), litter quality had a more significant negative welfare impact than stocking density [68]. Since substrate quality can pose challenges to bird welfare, preventative measures such as using different flooring types to replace or lay beneath the litter have been tested. However, research has produced inconsistent results, with some research finding behavioral and physical implications based on flooring type [30,62,69] and another study finding regular litter change to be the best welfare condition compared to different flooring treatments in poultry [70]. In zoo and aquarium birds, flooring and substrate are rarely studied. The impact of different substrates on air quality and individual preferences of flooring is valuable to consider. Regular maintenance of substrates, implementation of textured flooring, and proper ventilation can promote positive bird welfare within zoos and aquariums.

#### 4. Lighting

Most birds under human care live indoors with limited or no access outdoors [19,54]. Thus, the type and amount of lighting provided can impact their welfare. One study, which assessed ten resource-based measures across eighty-nine flocks of farmed chickens, found the length of the dark period to be one of the top three risk factors for poor welfare [66]. Shorter dark periods are linked to increased stress, negative emotional state, lameness, fearfulness, decreased bone development, impaired hormone cycles, and decreased weight gain [66]. Interestingly, the impact of lighting may be relevant as early as the embryonic stage, with proper light exposure during incubation influencing brain lateralization, post-hatch behavioral development, and possibly activation of the HPA axis [71]. Although zoo and aquarium birds may not experience a photoperiod as extreme as farmed poultry, the welfare implications of lighting are essential to account for, nonetheless. The successful development of circadian rhythms is considered an indicator of welfare across species, stressing the need to further study the photoperiod of zoo and aquarium birds [65,72].

Another consideration is the intensity of the lighting provided in zoos and aquariums. Generally, a light intensity of 20 lux is recommended to maintain optimal welfare for birds [73]. Low light intensities can result in eye abnormalities, reduction in activity and food consumption, and an increase in lameness and aggression in chickens [64]. When given the option to increase light intensity, chickens demonstrated a clear motivation for increased intensity [74]. However, just as artificial lighting can vary in intensity, it also varies in flicker frequency. Humans have a flicker fusion threshold of 50–60 Hz, whereas birds have one of more than 100 Hz [75]. As a result, passerine bird species in laboratories have shown altered behavioral responses, stereotypies, reduced activity, and higher basal corticosterone under low-frequency fluorescent lighting compared to high-frequency lighting [76]. A flicker frequency of above 100 Hz is suggested for optimal welfare conditions but needs further investigation across a variety of bird species [77].

A final consideration is ultraviolet (UV) lighting, which is produced naturally by the sun. Since birds have tetrachromatic vision, ultraviolet lighting is essential to their welfare, influencing behavior, biology, and physiology [78,79]. Behaviorally, UV lighting provides birds with information about their environment, assisting in mate choice, foraging, and parental care [76,80,81]. Physically, UV lighting can improve feather condition, aid in bone development, and decrease corticosterone in chickens [82,83]. One zoo study tested the preferences of 18 unique species ( $n = 67$ ) in a free-flight habitat to investigate if birds would choose areas of the habitat with UV lighting. Generally, the birds spent more time in the UV-lit area, which was speculated to have increased the birds' sociality, and there were noticeable behavioral differences based on the birds' natural ecological niche [78]. Multi-species studies such as this, which incorporate photoperiod, light intensity, and flicker frequency, are essential to design species-specific lighting schemes that simulate a bird's ecological niche in zoos and aquariums.

## 5. Sound Environment

Sound environments birds experience in zoos and aquariums can interfere with conspecific communication and lead to fitness issues [84] or alter behavioral and hormonal patterns [85,86]. Anthropogenic noises such as mechanical systems [84,87], or intermittent noises such as zoo visitors [88,89], lab processes [90], or transportation noises (trucks, trains, and airplanes) [91] can impact bird welfare. A study on soundscapes in a zoo measured a 29% increase in decibel levels when visitors were present [92]. Sporadic event noises such as construction [93], concerts [86,94], and educational events [95] have also been found to invoke responses. As animal welfare science evolves, monitoring an animal's response to sound stimuli is gaining traction [93,96,97]. There is a growing trend to acknowledge individual variability since noise can affect a bird's stress response differently, resulting in changes to physical and mental health, fitness, and behavior [84,86,93].

Anthropogenic noise can lead to behavior change in birds and potentially affect their welfare [93,98]. Extended events such as maintenance and concerts may impede bird communication resulting in possible chronic stress responses and reduced reproductive fitness [86,99]. Construction noises caused a pair of emus (*Dromaius novaehollandiae*) to increase stereotypic behaviors and alter their space use [93]. Visitor noise elicited location change, reduced range, and movement to ground vegetation in some of the 27 species residing in a free-flight aviary [88]. When subjected to sound recordings, birds in a multi-species exhibit changed flight and vocalization behaviors [98]. A multi-institutional study found that Chilean flamingos (*Phoenicopterus chilensis*) also altered their space use during a sound study but noted that their movement could have also been influenced by weather or visitor presence [100]. Like zoo-housed birds, laying hens also changed locations as a response to anthropogenic noise. However, poultry location change was coupled with extended durations of tonic immobility [91]. Additionally, non-enriching sound environments have been linked to feather pecking in poultry [91,101,102]. This can provide insight into peafowl welfare in human care since various species have been shown to spend approximately 13% of their time feather pecking [103]. Furthermore, sound may influence birds before hatching since sporadic loud noises nearby incubation chambers or nests have been linked to early hatching in poultry [87] and are suspected of causing nest abandonment in lesser flamingos (*Phoeniconaias minor*) [104]. Conversely, a quiet environment is a risk factor for apprehension, fear, and frustration in lab-housed Psittaciformes [90].

Current strategies to minimize the impact of anthropogenic noise on bird welfare emphasize spatial and temporal considerations [84] as well as an understanding of each species' hearing thresholds, including infrasound and ultrasound levels [105,106]. Recent literature suggests three strategies to reduce sound disturbance and improve bird welfare. One option is to change the noise source by reducing the frequency or amplitude of the emitted sound [96]. This could include adjusting the frequencies of infrasounds that can be heard by birds but are below a human's hearing threshold [107]. The second option is to alter the noise transmission by utilizing barriers or absorptive construction materials to affect what animals hear [93,96,106]. Finally, relocating or allowing animals the choice to relocate might reduce or eliminate the disturbance [93,96,106]. A continued empirical investigation into these methodologies in zoo and aquarium birds is necessary and will provide insight into best practices for managing sound environments. Given the findings across industries, zoos and aquariums should prioritize finding an optimal noise level for each species of bird to ensure they thrive in their environments.

## 6. Environmental Enrichment

Environmental enrichment is a common provision used to improve the welfare of animals by increasing environmental complexity and encouraging species-specific behavior [108,109]. Environmental enrichment for birds aims to increase activity and time spent displaying natural behaviors, improve health, and reduce the prevalence of undesirable behaviors [110–112]. Bird enrichment can consist of alterations to the environment, such as increasing the distance between feeders and drinkers, installing perches, presenting novel

objects, or providing nest boxes. Research on zoo penguins has found that different types of enrichment can reduce or prevent foot lesions, a common concern for many birds under human care [61,113]. When studying zoo-housed macaws and farmed chickens, the mere presence of enrichment resulted in positive behavior changes such as an increase in feeding, social interaction, general activity [114], stress resilience [115,116], and improved physical and mental development [101]. In other cases, the presence of enrichment items did not significantly change indicators of welfare such as behavioral diversity in gentoo penguins (*Pygoscelis papua*) [117] or the gait score, behavior, or mortality of farmed chickens [118]. Nonsignificant results could be due to the type of item presented, variability across species, or study design [117,118]. The inclusion of environmental enrichment for birds under human care can have far-reaching benefits but requires further research on the efficacy of the type and timing of enrichment and if it is successful in eliciting the behavior of interest.

It is generally accepted that behaviors such as roosting [119], nesting [41], dust-bathing [41,120], and swimming [32] are essential for a bird's emotional and behavioral welfare. However, there are many gaps in our knowledge about which enrichment items work best to increase these behaviors [109]. For example, one behavior that is used synonymously with positive welfare in chickens is dustbathing. It is thought that dustbathing is internally motivated to maintain feather condition, but limited research exists to show how enrichment can effectively increase the behavior [41,120]. Similarly, extensive evidence shows that chickens are motivated to access nest boxes, but these items are not regularly provided [31]. The inclusion of nest boxes and nesting materials could benefit the welfare of birds under human care since the vast majority nest in the wild. However, studies evaluating nest box designs or preferences for desirable nesting materials to determine the most effective models and materials are limited [41]. To satisfy roosting motivation in poultry, perches and elevated platforms are often supplied. Certain forms of perches have increased bone health and decreased aggression in chickens but should be used with caution since they may indirectly cause harm due to falls [41,109,112,121,122].

Providing birds with access to water has been consistently linked to improved welfare, especially in aquatic species [32]. Notably, the type of water access (e.g., a bath, a nipple drinker, shower, etc.) has varying impacts on duck welfare with water sources in which the birds can dip their heads and splash their feathers being optimal [123]. There is evidence that water baths are essential for bird health, aiding in feather maintenance, even in nonaquatic laboratory birds [76,124]. There is much opportunity to expand on this topic, particularly by considering the needs of nonaquatic zoo-housed species.

Foraging enrichment is also regularly linked to improved welfare in birds. Foraging enrichment includes devices that contain food and induce prolonged feeding time, different types of substrates (straw, peat, wood shavings, etc.) that increase scratching and investigative behaviors in terrestrial birds, and other items that engage birds in species-typical foraging behaviors [65,125,126]. Increased foraging opportunity through enrichment has been consistently found to improve feather condition in chickens and parrots by reducing feather damaging behavior [65,114,120,127,128]. Generally, there are two forms of feather damaging behavior: feather picking/plucking and feather pecking, distinguished by whom the behavior is directed toward, oneself or a conspecific. Feather picking or plucking is commonly seen in parrots and occurs when a bird plucks out one's own feathers, typically on the ventral wing, chest, and inner thighs, with mild cases resulting in feather loss and severe cases leading to hypothermia, infection, and skin and tissue damage [20,129–131]. On the other hand, feather pecking occurs when a bird aggressively plucks or pecks the feathers from another bird, typically displayed by farmed poultry, including chickens [28,132], pheasants [133], domestic turkeys (*Meleagris gallopavo domesticus*) [134], and ducks [32]. In extreme cases, feather pecking can lead to cannibalism [28,135]. In zoo and laboratory birds, foraging enrichment has not only prevented stereotypic feather damaging behavior but reversed it [76,126,136,137]. Additionally, it can decrease aggression among conspecifics and increase activity [125,138,139]. In zoos, scavenger birds, such as vultures, show a preference for natural foraging opportunities such as carrion [140]. The provision of carcass feeds also

increased time active and foraging in Southern ground hornbills (*Bucorvus leadbeateri*) [141] and Andean condors (*Vultur gryphus*) at multiple zoos [142].

Overall, enrichment that increases time spent foraging, can significantly improve a bird's behavior and physical condition. Enrichment is provided regularly in zoos and aquariums; however, there is a lack of research across bird species on which items are most effective at increasing natural behaviors other than foraging. In addition to evaluating efficacy, we can conduct motivation preference assessments to examine how much of a cost an individual is willing to "pay" to gain access to an item. For example, incrementally increasing the weight of a door that needs to be pushed to gain access to the desired item [143]. Zoos and aquariums would benefit from determining which behaviors birds are internally motivated to perform using environmental enrichment as a proxy.

## 7. Social Management

In the wild, birds generally reside in small flocks, and some species, typically Psittaciformes, form bonded pairs within a larger flock. Accredited zoos and aquariums strive to replicate a species' natural environment by housing animals based on their natural history [144]. However, this is not always the case with companion birds, farmed poultry, and birds in laboratories. Poultry are kept at high densities, measured by the number of birds or kilograms per square meter [145]. Birds kept in near-identical conditions with manipulated stocking density had worse welfare under the highest stocking condition (8 hen/m<sup>2</sup>) with decreased feather condition, production value, gait score, and greater mortality rates, consistent with previous findings [112,146–149]. In addition to high social densities, poultry are commonly kept in same-sex groupings with near-identically aged birds. Although birds at accredited zoos and aquariums are not typically housed in overcrowded conditions, the major welfare concerns resulting from such conditions are necessary to be aware of since species may react differently to social density. Additionally, zoo birds may be housed in same-sex flocks depending on breeding recommendations. When analyzing the social networks of multiple species of zoo-housed flamingos, it was found that individuals prefer socializing to solitary behavior regardless of exhibit size [150]. A multi-institutional study of great white pelicans found that individuals had lower corticosterone detected in their feathers when they lived in groups of ten or more compared to pelicans housed in groups with less than ten individuals [38]. Since natural flock numbers cannot typically be achieved in a zoo environment, determining a minimum number of birds per flock to achieve optimal welfare in gregarious species such as flamingos and penguins is necessary to inform husbandry practices and future exhibit design [26,45,151].

Laboratory and companion birds are often singly housed, and although zoos and aquariums work to avoid single housing of social bird species, it occasionally occurs. Many bird species show intrinsic motivation to interact or even remain in close proximity to conspecifics [152]. Undesirable social arrangements deprived chickens of natural social interactions that alleviated stress, decreased fear responses, and aided in coping with challenges [145,153]. Additionally, maternal care is limited or entirely forgone, depriving chicks of their earliest social bond, resulting in increased aggression, fearfulness, stereotypical behavior, and decreased feeding across industries and bird species [76,153–155]. Laboratory parrots housed in pairs engaged with enrichment more and spent less time preening, screaming, and inactive compared to singly housed birds [152]. Identifying how best to manage paired individuals is crucial since it can directly contribute to the successful reproduction of threatened species such as the critically endangered 'Alala (*Corvus hawaiiensis*) [156] and the threatened great hornbill (*Buceros bicornis*) [157]. Species-specific guidelines for social management are essential. Past experiments that tested the choice of environmental resources such as lighting and substrate can act as models for future research on social preferences and motivation to engage with differing flock sizes in zoo and aquarium populations [11,158]. Situations where it is impossible to manage birds based on their natural histories (due to genetics, aggression, etc.), should be examined

to determine how it impacts welfare. Information on optimal flock sizes for welfare and breeding success is critical.

### 8. Human–Bird Interactions and Relationships

The presence of humans inevitably impacts animals in zoos and aquariums. The study of this influence is common amongst zoological institutions since animals are exposed to animal care staff and visitors daily. However, only a handful of bird species have been studied in this context, and a clear impact, whether positive or negative, is difficult to determine [159]. For example, in Sphenisciformes, a positive influence of guest presence has been found and resulted in increased behavioral diversity [117], locomotion [160], feeding, and preening [161]. However, negative influences of visitors have also been discovered in the form of decreased pool use [162,163], increased fear-based behaviors, and altered space use resembling avoidance [162,164,165]. Although each species was of the same taxonomic order, the variation in results could be due to species-specific differences, variability in habitat design, or differences in study methodologies. When monitoring individuals specifically or considering multiple species, studies have produced mixed results with some individuals or species reacting to the presence of visitors and others showing no significant difference [166–169]. As crucial as negative and positive results are, nonsignificant results should not be overlooked and may suggest that visitors have limited or no impact on the behavior of some birds [88,170–174]. Consistency amongst visitor presence measures and their operational definitions is critical to tease apart conflicting results since it is measured in several ways. Additionally, studies considering visitor variables, environmental conditions, and habitat characteristics are essential [161,175,176]. Visitors can have an impact, positive or negative, on birds in zoological facilities; however, this effect has been almost exclusively studied in mammals, emphasizing the need to study diverse bird species [159].

The interaction between birds and their caretakers (animal care staff at zoos, labs, and farms, or the owners of pet birds) is an aspect of human presence that is frequently overlooked. Regular interaction between caretakers and birds is typical but has been very scarcely studied [159]. Cognitive research has found that parrots and passerines can distinguish between humans and formulate trust, which can significantly impact the husbandry and welfare of zoo-housed birds [177,178]. Specifically, human–bird trust could be beneficial during animal handling for health procedures, transportation, or education purposes [179,180]. A retrospective analysis of health examinations across animal taxa found that approximately 97% of all complications during bird health exams were minor wounds afflicted from handling and capture for the procedure [181].

In addition to health examinations, birds may be regularly handled and exposed to public guests at zoos for education purposes. In this context, it was found that handling itself was not linked to change in the fecal glucocorticoid metabolites (FGM) of zoo-housed red-tailed hawks (*Buteo jamaicensis*); however, the duration of handling was positively correlated with FGM, indicating that longer handling may impact adrenal response [182]. A large-scale phylogenetic study of Psittaciformes found that gentle handling and positive human–animal relationships result in lower corticosterone, decreased fear responses, and overall, an increase in production values [183–185]. Research with chickens as zoo program animals has found that experiences where guests approach the animals' home habitat for feeding interactions may not reduce welfare and created a valuable human–animal interaction without direct handling [186].

Another form of handling is artificial or hand-rearing, which occurs across industries for various reasons. In the context of companion animals, hand-rearing is commonly thought to create a deeper bond between the owner and their bird despite little evidence. Further, birds are incorrectly thought to be “low maintenance” pets. Owners are surprised if their bird begins to show adverse behavior such as aggression, fear, and stereotypes due to limited relationship building and improper care [155,187,188]. In laboratories and zoos, hand-rearing may occur as a last resort when the chick is rejected, or the mother bird

is unfit [189,190]. Several health risks are involved in hand-rearing, such as maladjusted birds, crop burns, aspiration, nutrition deficiency, increased rates of stereotypies, and even premature death [97,154,191].

Proper training is a possible solution to negative relationships between birds and their caretakers across industries. When animal welfare training amongst staff was implemented, several welfare indicators were positively impacted [192] despite rare instances in which staff behavior had no impact on poultry behavior and welfare [193]. In farmed ostrich (*Struthio camelus*) and zoo-housed kori bustards (*Ardeotis kori*), a positive relationship between birds and their caretakers seemed essential to their welfare [194,195]. The human–animal relationship is increasingly being studied as it is a criterion of one of the popular farm welfare assessment tools, The Welfare Quality assessment [196]. The results of improved human–animal relationships on poultry welfare are promising, but it is worth noting that a lack of domestication may impact the habituation of exotic species to human presence. Research is limited, but a positive human–animal relationship between birds and animal care staff and veterinarians seems pivotal to improved welfare. Understanding how visitors, animal care staff, veterinarians, and hand-rearing impact birds is essential to ensure high welfare standards in zoos and aquariums.

## 9. Genetics

Genetic manipulation is a welfare concern ubiquitous in agriculture but has implications for birds across zoos and aquariums that may experience indirect genetic manipulation through selective breeding [110,197]. Selectively breeding chickens for desirable physical and behavioral traits (or selecting against undesirable ones) is increasingly popular as housing regulations continue to evolve and change, presenting new challenges for producers [198,199]. Selection for expedited growth can result in genetic health issues such as disease, skeletal disorders, and reduced or inability to locomote [72]. Conversely, selection against undesirable behaviors such as feather pecking has reduced mortality and fearfulness in chickens [200,201]. As such, successful genetic selection against behaviors that are detrimental to bird welfare could impact birds across industries [199]. However, the unforeseen health implications cause researchers to question the sustainability and long-term effects of genetic selection across industries [54,110,202].

Intentional alteration of specific traits of zoo and aquarium birds is not practiced and not recommended for birds with conservation value [110]. However, there is evidence of unintentional genetic alteration of zoo birds in the form of genetic adaptation [203]. Due to this, programs that focus on reintroducing professionally managed populations are less successful when compared to those that use wild-born translocations [203]. Additionally, the scientific value of research produced from genetically altered birds (intentional or not) presents controversy since their cognitive functioning may be changed, and results may not be representative of the population [23]. Institutions that participate in breeding programs with the aim to reintroduce endangered bird species to the wild should practice caution and minimize the risk of genetic adaptation by reducing the number of generations a species spends in human care [203,204].

The natural history of a species may play a role in its ability to adapt to human care in addition to intentional genetic modification. Scientists hypothesize that naturally bold (less fearful), behaviorally flexible, invasive, non-migratory, less vulnerable species may have a higher coping capacity [144]. A large-scale study of over 700 individual parrots under human care discovered that species that are ecological specialists with innovative, prolonged natural foraging efforts [205], larger brain volumes, and compromised conservation statuses have higher frequencies of abnormal behaviors, including feather damaging and oral-focused stereotypies, decreased reproductive rates, and difficulty breeding [20]. However, natural group size was not a significant predictor of reduced welfare, and none of the examined natural biological variables predicted susceptibility to medical problems [20]. A follow-up study found that Psittaciformes with large brains were most susceptible to stereotypes, including route tracing, head-twirling, and bar biting, suggesting that intelli-

gence can be an indicator of welfare status [206]. Recent research, which compared different breeds of chickens used for production, found that breeds tend to have better welfare under the specific conditions for which they were genetically selected and may have reduced welfare in conditions that deviate [53,207–209]. Further, there is evidence that some strains may be more prone to lethal infections and disease [210]. While this research is sparse, animal care staff, scientists, and other zoo personnel should consider how the natural history of a species might influence its welfare under different conditions [211–213]. In zoos and aquariums, birds with high adaptability to human care may have increased reproductive success resulting in the genetic overrepresentation of such individuals. Although not intentionally genetically selected, this could lead to the sustainability issues and welfare concerns identified in other industries.

## 10. Nutrition

Bird nutrition has evolved from simply addressing hunger and thirst as part of the original Five Freedoms framework to prioritizing the opportunity to be “thoughtfully presented a well-balanced diet” as part of the Opportunities to Thrive framework [2]. Under the Five Freedoms, birds can be free of hunger and thirst while also malnourished. For example, approximately 90% of all clinical conditions in companion parrots stem from malnutrition as many diets are high in fat and lack required nutrients [155]. For this reason, accredited zoos and aquariums strive to create species-specific diets that meet each species’ nutritional and behavioral requirements [214–217]. However, in the past, it was common to supplement less-studied bird species’ diets with well-studied species’ [218,219]. This is not ideal for optimal bird nutrition, health, and welfare. For example, a diet based on poultry research is an inappropriate template for psittacine birds since their energy, protein, and calcium requirements are lower in all stages of life [219,220]. Additionally, substituting nutritional requirements from better-researched species such as budgerigars (*Melopsittacus undulatus*) or cockatiels (*Nymphicus hollandicus*) is not always appropriate [219]. A study of Loriinae species reiterated this concept when results revealed that birds from the same family have regional differences that affect their nutritional requirements [218]. Zoos and aquariums must create species-specific, well-balanced diets based on data from research and regionally available food sources [214–216,218].

Creating a nutritionally complete, species-specific diet requires integrating a bird’s ecology and biology while working collaboratively with animal care and veterinary staff to understand how species-specific nutritional requirements, health status, habitat, husbandry protocols, and animal preferences are interconnected [214,215]. Nutritionists must choose from over 64 essential nutrients while accounting for quantities and ratios of nutrients to create each individual’s diet [214]. The calcium to phosphorus ratio is frequently cited as essential to skeletal health and egg quality [215,216,221,222]. Nutritionists must be cognizant of how a bird’s nutrient intake and behavior can be affected by methods of food storage, preparation, and presentation [215,223]. For example, storing mice in freezers reduces their vitamin E content, thereby altering the nutrient intake for carnivorous birds [224]. Even minimal preparation, such as chopping, could affect the rate of nutrient breakdown or moisture content of food, as evidenced by human food-science studies [223]. When fruit preparation changed from chopped to whole fruits, blue-and-gold macaws (*Ara ararauna*) increased their fruit intake by approximately 39% and their activity budgets changed [225]. Additionally, Psittaciformes, which spend a large portion of time handling and manipulating food in the wild, were more prone to feather damaging behaviors when compared to other phylogenetic traits [206]. This suggests that these species are given diets of inadequate complexity or composition in human care [206]. Food presentation is often dictated by training and behavioral needs, requiring special attention to ensure nutrient intake is not compromised by husbandry protocols [214,226]. Preparation methods, presentation strategies [214,215,223], and misunderstood nutritional requirements can lead to deficiencies or toxicities [214] and impact welfare if not appropriately managed [215].

Nutritional deficiencies are often managed with dietary supplements that can be given proactively to address a known health problem [215,227] or behavioral issue [228]. Research addressing the links between nutrition, supplements, and pododermatitis in poultry determined that protein intake affected the condition [229], but iodine-treated water [230] and zinc supplements [231] could reduce the issue. Foot conditions are not unique to farmed birds and are commonly found in zoo birds such as flamingos and penguins [58,61]. Reduced zinc absorption is speculated to contribute to pododermatitis in flamingos but requires further study before dietary recommendations can be made [217]. In addition to impacting health, supplements can affect behavior [228,232]. Poultry research suggests that supplements containing probiotics for gut health might improve the behaviors of birds under heat stress [232]. Supplemental zinc and calcium have been linked to increased dust bathing and sexual activity, decreased aggression, and lower corticosterone levels in poultry [228]. Unmanaged deficiencies can have lasting effects. Passerines that experience nutritional deficiencies early in life have impaired song development and spatial memory as adults [76,211]. Carotenoid and copper deficiencies can impact reproduction since they affect feather coloration and, in turn, influence mate selection [215,216,233]. Deficiencies can also be the unintended consequence of individual preference assessments meant to understand a bird's nutritional requirements [214,219,234] but assume birds will select foods with nutrients needed for a proper diet [218,234]. However, selecting for taste or presentation has been found [221,235]. The wide array and intensity of consequences resulting from nutritional deficiencies validate that creating species-specific diets needs to be a collaborative and proactive effort between nutritionists, ecologists, veterinarians, and animal care staff.

Opposite of deficiencies, nutritional excesses or toxicities can also be problematic to bird welfare [214]. Excesses can result from a lack of understanding of the specific needs of a species, commercial feed issues [214], or bioaccumulation [236]. For example, iron storage disease, which results in the accumulation of toxic iron levels in the liver, is common in some bird species that are more efficient at absorbing iron and lack regulating processes [224,237,238]. An improperly labeled commercial feed can lead to toxicities, reduced welfare, and mortality [237,239]. Additionally, feeding birds unvaried diets increases the risk of bioaccumulation. Compared to their wild counterparts, zoo-housed seabirds fed unvaried diets had more accumulation of heavy metals, which increases their risk of neurological deficits, reproduction issues, skeletal abnormalities, iron storage disease, and reduced growth rates [236]. Zoo and aquarium bird welfare will benefit from a better understanding of how various species metabolize individual nutrients, how nutrients affect behavior and health, improved quality control protocols for commercial feed, and investment in species-specific diets.

## 11. Welfare Assessments

Throughout the review, we have highlighted how resource-based measures (inputs) can impact animal-based measures (outputs) such as bird health, physical condition, behavior, and emotional state. When creating an ideal welfare assessment, scientists should combine inputs and outputs for a holistic approach. Assessments that only monitor resource-based measures can miss essential cues from an animal's behavior, and strictly monitoring animal-based measures can overlook environmental components of influence [240]. For instance, researchers found that monitoring variations in feather-ruffling of Sulphur-crested cockatoos (*Cacatua galerita*) can provide a non-invasive, visual indicator of calm states, increasing the number of positive welfare indicators for birds [241]. While cognizant of the information presented here, future research can assess bird welfare using established comprehensive frameworks such as the Opportunities to Thrive or the Five Domains Model [240]. These frameworks will be especially useful when designing preliminary welfare research focusing on scarcely studied species. Much of this review pulls from the agriculture industry, which also has a host of welfare assessments that can be adapted for zoos and aquariums. One of the most popular is the Welfare Quality As-

assessment, which evaluates four principles (good feeling, housing, health, and appropriate behavior) by considering animal-based measures such as physical health and expression of social behavior [242]. Adapting measures primarily used in agriculture can give a unique perspective on the welfare of zoological birds.

## 12. Conclusions and Future Directions

The information contained in this review provides insight across industries on the welfare of birds under human care to be applied to zoo and aquarium birds. This knowledge can be used by animal care staff to proactively manage species under their care or by scientists when considering the next steps for research. As seen throughout, approaches to the assessment of bird welfare vary significantly across industries. Agricultural and laboratory research tends to focus on broad concepts of the welfare of a collective group, benefiting from large sample sizes across semi-similar environments and the ability to systematically and experimentally manipulate variables. In zoos, studies tend to focus on complex questions of individual welfare and can survey diverse species. However, sample sizes remain small, experimental manipulation is rare, and generalization can be difficult [243]. Nevertheless, the diversity of species in zoos and aquariums is an opportunity. Instead of separating industries based on their differences, researchers should welcome the deviations to gain a new perspective on how to best monitor and improve bird welfare within zoos and aquariums [14].

The reviewed literature suggests that bird welfare is gaining priority within zoos and aquariums, but much remains to be discovered [5]. The most significant area of opportunity for studying bird welfare in zoos and aquariums is the diversification of study species across all topics of welfare research. Diversification will increase the representation of understudied species and allow for investigation into how natural history characteristics impact bird welfare [20,25,144]. Most bird welfare research focuses on a handful of species. Although research findings may be applicable across species, studying a diversity of species cannot be understated. Future research can utilize large data management platforms such as Species360 Zoological Information Management Software Release 20 April 2022 (Minneapolis, MN, USA) to assess bird welfare based on natural history characteristics across hundreds of institutions and species [144]. Additionally, the knowledge of wild bird populations can inform best practices for understudied bird species [244].

Validating commonly accepted notions and practices with empirical evidence should be prioritized, especially across underrepresented bird species. For example, evidence suggests that providing environmental enrichment is beneficial and, in turn, is regularly practiced [108]. However, the efficacy of specific items and timing of enrichment is rarely examined scientifically, even though it would likely increase welfare and save staff resources [111]. Likewise, flight management procedures such as pinioning and wing clipping are speculated to reduce welfare. These procedures are banned entirely in some countries, but the evidence is sparse, inconsistent, and only covers a handful of species [35]. Future research should compare the impact of flight itself and flight-restricting procedures on welfare across species and zoological institutions where those methods are practiced [35,39].

Further investigation of disregarded areas such as nutrition, sound environments, lighting, and flooring is necessary since each can drastically impact bird welfare. Nutrient composition [214,216,236] and diet preparation and presentation [223] are crucial considerations moving forward because they potentially influence nutrient content, contamination, and illness [223,245,246]. Zoos should continue to focus on creating diets that are species-specific [218], account for physiological status [215], strive to increase species-specific foraging behaviors, and fulfill the nutrient requirements of birds through all life stages [151,247]. Additionally, a better understanding of species-specific traits such as hearing [106] and flicker fusion thresholds [77], vocal plasticity [99], light intensity needs [248], and optimal UV exposure [78] will help us understand the influence of noise and lighting on bird welfare. Finally, the impact of substrate and flooring on zoo bird

welfare has been repeatedly overlooked, even though this topic is regularly studied in the poultry industry and can contribute to many health risks [62]. Agricultural studies can be used as a starting guide to design future research on how different substrates affect air quality and bird welfare, as well as individual preferences for flooring and substrates in zoos and aquariums.

The current review took an applied approach by evaluating resource-based measures. The assessment of these measures is essential, but future research on animal-based welfare measures is equally necessary since it is almost obsolete in birds and scarce even in mammals [151,249,250]. For example, the physical complications of feather damaging behaviors are obvious but research investigating how the behaviors impact a bird's affective state can provide novel insight and solutions [251]. Recent research has found that a parrot's emotional state may be predicted by something as simple as facial feather-ruffling [241]. Identifying how feather positioning on the face and body translates to emotion is a promising use of animal-based measures in birds [16,178,252]. However, it is still challenging to interpret what commonly used behavior indicators mean for an animal's affective state. With the increasing use of technology and the popularity of precision livestock farming, evaluating affective states may be closer than previously thought [253,254]. While negative behaviors need to be alleviated, we cannot achieve optimal welfare if we are not also working to increase the prevalence of positive behaviors [2,3,255,256].

Birds provide a unique challenge for behavioral monitoring since they are typically housed in flocks, making it difficult to identify individual birds and record their behavior [257]. Due to such challenges, leg bands are commonly used, and technology is becoming increasingly common, particularly in welfare science. Automated technology that records behavior without the necessity of a human observer can provide information on space use [258], nocturnal activity [259], morphology [260], fear and pain [261], feed intake [262], locomotive patterns to detect health issues [263–266], early warning signs of harmful behaviors [258,267], and improve husbandry and reproductive output [268]. The opportunity to cater to animals individually rather than at the flock level is more realistic with such technology. Wearable devices such as radio-frequency identification tags (RFID) [269] and time-depth recorders [270] provide unique insight into individual bird behavior and social interactions. In conjunction with technology and other indicators, physiological advancements present an opportunity to incorporate additional welfare and health measures [169,243]. A bird's physiology can be recorded through droppings, feathers, or blood [271,272]. Physiological measures contribute empirical information about a bird's stress levels and personality traits [273]. In addition, a bird's physiology gives essential insight when interpreting behavioral data [243,274–277]. When monitoring over 200 pelicans, fluttering behavior was significantly associated with higher corticosterone levels in feathers, suggesting this behavior could be an animal-based indicator of negative welfare for this species [38]. Future research should supplement behavioral indicators with physiological measures and novel technology for optimal, multi-faceted results.

Although we are just beginning to scratch the surface of bird welfare research in zoos and aquariums, there are abundant future research opportunities informed by outside industries such as agriculture, laboratories, and companion animals. Zoos and aquariums should strive to prioritize bird welfare research through species-specific assessments across diverse species, empirical evaluation of standard practices and environmental factors, phylogenetic comparisons, and incorporation of novel technologies, physiological measurements, and animal-based indicators. Hopefully, this review will inspire researchers and animal care staff to improve bird welfare by diversifying study species, collaborating among zoological institutions, and innovating and integrating knowledge from all industries that care for birds.

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