birds

Commentary

Considering What Animals "Need to Do" in Enclosure Design: Questions on Bird Flight and Aviaries

Paul Rose [1,*], Marianne Freeman [2], Ian Hickey [3], Robert Kelly [1] and Phillip Greenwell [4]

1 Centre for Research in Animal Behaviour, University of Exeter, Exeter EX4 4QG, UK; rk528@exeter.ac.uk
2 Sparsholt College Hampshire, University Centre Sparsholt, Sparsholt, Winchester SO21 2NF, UK; marianne.freeman@sparsholt.ac.uk
3 Chester Zoo, Upton-by-Chester, Chester CH2 1LH, UK; i.hickey@chesterzoo.org
4 Salce, 32430 St. Georges, France; phillipjohngreenwell@gmail.com
* Correspondence: p.rose@exeter.ac.uk

Simple Summary: Flight is a fundamental characteristic for the majority of bird species, but how well is this behaviour catered for when birds are housed in managed populations under human care? Zoo enclosure design and animal care practices often balance natural behaviour performance and what is feasible in a human-made environment. As zoos focus more on animal welfare, enclosures should be evaluated to ensure they provide adequate space, natural habitat features, and opportunities for natural behaviours. This paper highlights the need for a better understanding of behaviours, using flight in bird as the core example, and recommends posing and then answering directed questions to gather evidence for improved enclosure design to provide for what birds need to do. We call for changing "best practice" guidelines to "better practice guidelines" to emphasise continuous improvement in animal care based on evidence and regular reassessment, and to encourage all stakeholders in zoos to regularly consider the impacts of housing and husbandry on animal behaviour and welfare.

Abstract: Zoo enclosure design, and housing and husbandry protocols, will always be a compromise between what a species has evolved to do and what is possible to offer in a human-created environment. For some species, behaviours that are commonly performed in the wild may be constrained by husbandry practices that are used for ease or aesthetics or are accepted conventions. As zoos place more emphasis on positive animal welfare states, zoo enclosures should be scrutinised to check that what is provided, in terms of useful space, appropriate replication of habitat features, and maximal potential for natural behaviour performance, is relevant to the species and individuals being housed. For some species, zoos need to grapple with tough questions where the answer may not seem immediately obvious to ensure they are continuously improving standards of care, opportunities for the performance of species-typical behaviours, and advancing the attainment of positive welfare states. Determining the importance of flight, for example, and what this behaviour adds to the quality of life of a zoo-housed bird, is an important question that needs addressing to truly advance aviculture and how we determine bird welfare. This paper provides questions that should be answered and poses measures of what flight means to a bird, to provide evidence for the development and evolution of zoo bird housing. If we can devise some way of asking the animals in our care what they need, we can more firmly support decisions made that surround enclosure design, and housing decisions. Ultimately, this means gathering evidence on whether birds like to fly (e.g., from birds in training or demonstration activities) by applying mixed methods approaches of behavioural analysis, data on wild ecology, qualitative behavioural assessment, and cognitive bias testing to develop a robust suite of tools to address avian welfare considerations. Avian welfare scientists should attempt to define what meaningful flight is (i.e., flight that truly suggests a bird is flying) in order to support guidelines on aviary dimensions, space allowance, and welfare outputs from birds in both flighted and flight-restricted populations, and to determine what is most appropriate for an individual species. Changing the term "best practice" husbandry guidelines to "better practice" husbandry guidelines would instil the importance of regular review and reassessment of housing

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and management suitability for a species to ensure such care regimes remain appropriate. With an increasingly welfare-savvy public visiting zoos, it is essential that we seek more evidence to support and justify how birds are kept and ultimately use such evidence to enact changes to practices that are shown to infringe on avian welfare.

Keywords: bird; enclosure design; aviary; welfare; animal behaviour

1. Introduction

Animals in zoological collections are managed within environments that are completely created by humans. A consequence of this is that there are some constraints on behaviour patterns or restrictions to time-activity budgets. For most zoo-housed animals, there will likely be a compromise between the logistics of managing the species and enabling the widest possible diversity of ecologically relevant behaviours. Whilst restriction on some behavioural performance may be a given, any compromise to welfare does not need to be. Ensuring complexity within an enclosure promotes behavioural diversity [1,2], which can uphold positive welfare outputs [3]. Aligning the complexity of an enclosure with elements of a species' ecology, therefore, provides for key behavioural needs and ensures the long-term relevance and currency of a zoo's exhibits. It is also important to remember that free-living animals in natural systems are not removed from restrictions to behavioural performance. Home range or territory sizes, competition from other animals, resource allocation and distribution, predation, disease, and social system will all restrict what animals can do at a specific time and place [4]. Our understanding of how animals can be behaviourally flexible to cope with such pressures is the essential information needed when evolving the design and format of captive management regimes. As we use an evidence-based approach to design and implement housing and husbandry [5,6], we can be more assured of the suitability of animal management regimes for the species that they are applied. Evidence can be gathered by using pre-existing concepts such as Tinbergen's Four Questions [7] and applying the questions of causation, development, function and evolution to wild behaviours and captive time budgets to evaluate why and how behaviour is performed, and what the animal gains from it [8,9]. However, there are still key areas of species' ecology that we do not fully understand and therefore our care for these species in ex situ populations is a compromise. One such example of this ecological "grey area" is whether birds like to fly.

Animals in zoos need to be enabled with choice (over what they can do and where they can be) and control (over their immediate internal and external environment) as this provides them with a feeling of autonomy and agency, which are important for attaining positive welfare states [10–12]. Birds in zoos may be denied key elements of choice and control due to the degree of constraint over their flying abilities. If animal welfare is defined as the state of an individual attempting to cope with its environment [13], and this concept is extended to include physical, behavioural, and psychological measures based on the animal's engagement with inputs and their impact on outputs [14,15], then bird welfare may be compromised if they are reaching for specific behavioural outputs that they are unable to fulfil due to the style of their enclosure or aviary, or management system.

Of the estimated 11,000 species of birds, approximately 99.5% are capable of flight [16]. Bird evolution has been largely shaped by flight [17], demonstrating the importance of this activity to their life, history, and ecology. A wide range of bird species are housed in zoological collections [18] and estimations of bird diversity in captivity suggest that all major orders of bird, except Phaethontiformes, are present in zoological collections [19]. Therefore, research into their housing and husbandry (to ensure these are fit for purpose and align with species-specific needs) benefits many hundreds of individual birds in zoos globally. If promoting well-being becomes a fifth aim of the modern zoo [20], then promoting positive welfare states for all zoo-housed species (and associated performance of species-typical, biologically relevant behaviours) must be a core philosophy of enclosure design, and associated housing and husbandry practices.

When considering bird enclosure design, zoos should be mindful of public opinion and what appears acceptable. Zoo visitors are becoming more aware of how animals live in the wild from increased exposure to different forms of media. Therefore, any mismatch between how a species is maintained and what is observed in free-living individuals needs to be explained and justified or reviewed and revised. For example, large birds with wide wingspans, evolved for soaring flight, that are prevented from doing this in an aviary may not display behavioural indicators of compromised welfare, yet could appear frustrated and bored to zoo visitors or be housed in a way that does not promote their natural ecology, conservation message, and evolutionary adaptations (Figure 1). Such data from wild ecology and natural history provide the foundation for designing enclosures in a way that promotes the use of adaptive traits and their conservation across generations [21]. Measuring both the bird's responses to their housing design via assessment of behavioural outputs and other associated welfare measures and asking questions of the zoo visitor to understand the impact (positive or negative) of such exhibits, informs practices for species-specific aviary design moving forward.

Figure 1. Movement patterns and daily travel time in flight should be quantified so that aviaries can accommodate the behavioural needs of birds when housed under human care. For some species, such as the Andean Condor (*Vultur gryphus*), providing flight opportunities that enable a similar extent of travel in an aviary may be very challenging to accommodate and enclosure designers need to be creative and consider how habitat replication and subsequent behavioural responses to such an environment can be produced in the zoo to provide for important behaviour patterns. Wild condor image free to use under Pixabay licence, photo credit: CarlosJM81.

Data from field ornithologists on how birds live is essential to the success of conservation action [22], reintroduction programmes [23], and to advancing our understanding of the functionality of traits that birds possess [24]. Training birds to promote adaptive behaviours essential to life in the wild, such as the ability to flock together, evade predators, and navigate a landscape when in flight, are all supportive of good survivability in the wild [25]. Brightsmith et al. [25] state that captive Blue-and-Yellow Macaws (*Ara ararauna*) must be provided with free-flight opportunities to enable full engagement with the environment. Such approaches should be considered for other birds, and their behavioural responses to opportunities for flight measured. Therefore, zoos should integrate such wild information in better (currently best) practice husbandry guidelines to identify exactly why housing and husbandry have been created in that specific way. A key aim of this paper is to pose research questions that should be answered to underpin the credibility and validity of best practice approaches to husbandry so that birds are exhibited in a manner that (i) enhances the range of natural behaviours that they can perform, (ii) promotes the experience of positive welfare states to the fullest, and (iii) engages visitors with conservation education messages. Our overall goal is to examine to what extent bird flight, and any need to fly, is considered in their management and husbandry (with a particular focus on aviary design) to improve their care in zoological institutions.

2. Determining the Importance of Flight to Birds

"Do birds like to fly" is a question deliberated in the scientific literature [26] as well as the welfare-centred query, "What happens when birds cannot fly" [27]. Scientists must continue to wrangle with this question and find ways of inferring the importance of flight to birds from a behavioural and welfare perspective. A Tinbergian approach, in the manner of Mellor et al. [28], to "Should birds fly" in the zoo may be required.

The framework of Tinbergen's Four Questions provides an unbiased and objective way of understanding the importance of behaviour to the individual and to the population overall [29], which can support applied research into welfare needs, for example [9]. Mellor et al. [28] illustrate how the identification of proximate causes of abnormal repetitive behaviour in captive birds, (e.g., from early life experiences or internal causal factors) as well as ultimate consequences (such as how abnormal behaviours may enable coping with a poor environment in the short term), help determine why some behaviours predominate in captivity and what the long-term impacts of their performance may be. Potential research questions that could be posed to aid our understanding of what birds get out of flying could focus on the following concepts which are outlined in Table 1.

Table 1. Research questions that need addressing to enable our better understanding how important the act of flying is to birds housed under human care.

Research Question	Reasoning	Disciplines Involved
Working for a reward (e.g., probability of expending effort to access a larger space for flight).	If an individual bird is prepared to expend time and energy to access a space for flight (e.g., solve a species and individual appropriate puzzle or manipulate the environment to enter into a larger space for flight from a smaller more restricted environment) this could indicate the strength of their behavioural need to engage in flying.	Laboratory-based study to evidence housing in the zoo.
Use of height when provided with aviaries of differing dimensions.	If birds choose to perch or fly at the highest possible elevation of an aviary (when this is available), this suggests a preference for height when using the space they are provided with.	Multi-zoo study to determine better practice approaches.
Purpose or reason for flight in the wild.	Defining the reason for flight (e.g., via a Tinbergian approach) and therefore the other behavioural outputs that use of flight enables when performing by free-living individuals of a specific bird species means we would have knowledge of why flight is used and what a bird gains from it.	Wild data collection and/or systematic review of the literature to support better practice in the zoo.
Reliance on flight as an escape or anti-predatory mechanism.	To better understand a bird's flight response, and therefore the space a bird needs to feel comfortable within an enclosure. Resources can then be placed within such areas to reduce a bird's chances of feeling threatened by stimuli, such as visitors or keepers.	Wild data collection and/or systematic review of the literature to support better practice in the zoo.
Propensity of the species to engage in play or flight within a social context (e.g., not just travel time in the air).	Measuring play will provide evidence for any social or pleasurable context of flight and therefore how much space, and how many individuals within a social group, needs to be provided to enable the performance of such activity so birds can experience the benefits from it.	Wild data collection and/or systematic review of the literature to support better practice in the zoo.

Table 1. *Cont.*

Research Question	Reasoning	Disciplines Involved
Number, distance, and duration of distinct flights per day around a home range or territory.	Calculation of the time a bird spends in the air will enable the normality of in-zoo time activity budgets to be judged and provide information on required amount of space to enable to such flight time to be performed.	Wild data and multi-zoo data collection.
Degree of migratory urge.	Determining whether the species is likely to display a change in behaviours (e.g., restlessness, heightened alertness, or more activity) at certain times of the year that is associated with a need to migrate. An enclosure could then be flexible to provide outlets for this increased urge to fly, for example offering more open space to enable flapping flight.	Wild data collection and/or systematic review of the literature to support better practice in the zoo.
Differences in time-activity budget of birds within different aviary spaces—what behaviours predominate if a species of bird is unable to perform a meaningful amount of daily flight.	Comparative review of time-activity budgets to determine positive behavioural diversity when a specific species of bird is maintained in different forms of enclosure. Choice to fly and perform aerial activity can be measured to see which ecologically relevant activities predominate when birds are given the space to access resources at different heights.	Multi-zoo study to determine better practice approaches.
Degree of lethargy or inactivity for birds in flight restricted conditions.	As an extension to the question above, to identify potential indicators of welfare that result from restriction on behaviour patterns. If birds are more inactive when housed in restricted conditions compared to in aviaries where meaningful flight is enabled, there is evidence for the type of space that is needed for that species and therefore the style of housing that should be provided.	Multi-zoo study to determine better practice approaches.
Probability of over-preening or feather damaging behaviours, and or/locomotory stereotypic behaviours when flight is restricted.	Performance of abnormal repetitive actions may increase when highly motivated activities are restricted. Birds may also redirect time to feather care and other self-directed actions if they are unable to fly or travel. Measurement of the proportion of time spent on abnormal and self-directed behaviours by enclosure type would indicate which form of housing reduced or eliminated the occurrences of such actions.	Multi-zoo study and/or phylogenetic comparisons to determine better practice approaches.
Any degree of morphological difference between populations of a species housed in different flighted or non-flighted environments.	Adaptation to captivity may result from unintentional directional selection imposed on a population from the environment they are exposed to. Review of wild biometric data, plus that from zoos and museums can identify which traits have altered in size or shape based on how birds are managed in zoos.	Wild data collection, museum data collection and zoo data collection to support better practice in the zoo.
Performance in cognitive bias testing and measuring anticipation before and after periods of flight to assess pessimistic or optimistic motivational states.	Measuring the effect of flight on positive emotions and moods by using judgement bias to determine underlying positive or negative moods from the bird's current condition. Birds that display more positive responses after flight is suggestive of them experiencing better welfare. Measures of anticipatory behaviour (e.g., perch-to-perch hopping, or attempted take-off) before a flying event could help define an optimistic outlook based on the opportunity to fly.	Integrating laboratory-based methods into multi-zoo study.

Table 1. *Cont.*

Research Question	Reasoning	Disciplines Involved
Longitudinal study to compare welfare measures in an individual bird that were previously flight restrained (e.g., feather clipped) to a situation where the same individual can fly (e.g., after a move into an aviary).	Measuring how a bird perceives the value of flight after a period of flight restriction would provide information on how keen a bird is to fly and what negative welfare indicators may be present when flight was previously restricted. Moving birds into new aviaries (when they may be feather clipped to enable them to acclimate without injury) would provide a good system for testing this.	Multi-zoo study to determine better practice approaches.
Measuring physiological change associated with flight and considering which endocrine markers could be indicative of positive physiological challenge when placed in an environmental context.	Contextualising measurement of behaviour and faecal corticosterone metabolites to consider all impacts on physiological change (such as presence of conspecifics, time since feeding, weather condition, and number of visitors) may provide a way of unpicking variation in corticosterone metabolite concentrations and a bird's choice to fly or not.	Integrating laboratory-based methods into multi-zoo study.

The questions posed in Table 1 can be answered by collaboration between zoos, and between zoos and academic or research institutions, as well as with field biologists who are collecting data on free-living birds. Cross collaboration between different animal industries can advance how welfare is measured, and the results of such measurement enacted upon [30]. For example, experimental designs used to document how much effort Domestic Hens (*Gallus gallus domesticus*) are prepared to expend to reach and enter a nest box [31], could be adapted and manipulated for behavioural studies with flying birds to quantify the value of a flight space based on energy expended to access it. Similarly, a controlled study in the laboratory using common research species –Zebra Finches (*Taeniopygia castanotis*), Bengalese Finches (*Lonchura striata domestica*), Common Starlings (*Sturnus vulgaris*), or Japanese Quail (*Coturnix japonica*), for example [32,33]—could be used to see the longer-term effects (across generations) of flight restraint. Housing birds in aviaries of different sizes (whilst still adhering to a species' minimum requirements) that would confer different degrees of restriction on flight behaviour and aerial movement would provide empirical evidence on how such environmental constraints impact individual bird patterns, as well as how individuals may cope in the long-term and what may impact their fitness. Welfare indicators, such as the performance of stereotypic behaviours, are known to be impacted by the cage size and shape that a laboratory bird experiences [34]. Research on Common Starlings indicates that both increased cage size and length provided the most noticeable improvements in bird behaviour patterns [34]. The methods from such research could be applied to similar set-ups using other laboratory birds (of non-passerines as well as passerine species) and any resulting data be extrapolated to zoo housing to show the longer-term positive impacts of enabling as much flight as possible on individual behaviour and welfare, and on the conservation of adaptive traits within a population.

Ensuring that enclosures in zoos are designed with futureproofing in mind can only be achieved through the collection and application of evidence. This evidence can come from observations of birds in zoos to see how their behaviour is impacted, for example, flight-restrained waterfowl (Anseriformes) can be more inactive than their wild counterparts [35]. Evidence shows that wild birds who regularly engage with human-created resources (e.g., bird feeders) diverge in trait morphology compared to birds living away from human influences [36]. Museum specimens can therefore be essential to our understanding of the adaptive traits that birds possess [24] and comparing the morphology of zoo-housed birds with those from wild populations may be specifically important for determining any potential adaptation to a human environment. If a bird species is housed in a way that restricts the behaviours it can perform, or if these captive individuals engage with environmental cues differently to free-living animals, and these changes convey an advantage for reproduction, a "zoo form" of bird may develop that could have more limited relevance to wider conservation initiatives, (see Tanimoto et al. [37]). Setting up directed research to answer the questions presented in Table 1 would add clarity to decisions made surrounding appropriate enclosure and housing design for birds and help support population sustainability.

Alongside flight, birds also use their wings for many other purposes, such as courtship display, threat responses, and communication between individuals. Any change to morphology due to constraints on flight may therefore impact on a wider suite of behavioural outputs, not just the ability to locomote and travel. Consideration of zoological records, such as those managed by Species360 on the Zoological Information Management System [38], for the length of time a species has been housed in captivity could provide useful data on reproductive outputs and what populations are breeding. A review of the husbandry and housing of such populations would then identify whether individuals that are breeding are those that have adapted accordingly, that the set-up is ecologically sound, and that birds are responding in a wild-type manner.

There is a clear conservation requirement to keep birds in ex situ populations [39,40]. Consequently, species-specific needs must be used as the basis for husbandry guidelines and enclosure design. The best way for some birds to experience good welfare may be in a flight constrained manner. For example, species of waterfowl such as swans (e.g., *Cygnus* sp.) and geese (e.g., *Anser, Branta* sp.) that use large expanses of water, that are terrestrial and graze on land may experience a better overall quality life (across the whole of their captive lifespan) being contained by feather trimming [41] rather than if they were housed in a covered aviary that still would not enable meaningful flight. Comparative studies of the behaviour of species of large-bodied waterbird (for example) between different housing styles (aviary or open-topped) are required to understand the impacts of (i) enclosure type, (ii) potential for any flight, (iii) overall useable space and (iv) variety of resources provided between enclosure styles on bird behaviour patterns and behavioural diversity.

3. Quantifying What Flight Is Meaningful to a Bird in an Aviary

If we are to assess whether an enclosure can provide for a bird's flight as an input to support positive welfare outputs, we need to define and then determine what type of flight is meaningful to the bird itself. By defining what flight is meaningful, we can then judge the overall net effect of animal management practices on animal welfare states; such an approach is essential if we are to understand what resources, environmental features, etc. are relevant to the individuals themselves [4]. Birds fly in different ways. Some species must perform constant flapping flight to remain airborne [42], others can hover [43], glide, and soar [44]. Some species have a "bounding flight" of a mixture of flaps and short glides [45]. Zoo aviary designers need to consider the type of flight a species uses when situating resources and furnishings within an enclosure, and zoo scientists must be considerate of such different flying styles and the reason for their evolution when attempting to determine what flight is meaningful. As such, defining meaningful flight could be based on the following considerations and measures, outlined in Table 2.

Figure 2 suggests measures of meaningful flight that could be taken to compare (i) when individuals of a species are maintained in aviaries or enclosures of different styles; (ii) how much time they spend in the air; and (iii) what form of flight is possible. Such an approach of "asking the animal" provides useful information for future enclosure designers on the size, scale, and scope of aviaries for specific species of bird to allow flight to be possible in the same way as experienced by free-living individuals. These questions of meaningful flight are currently unanswered in the scientific literature, and a consensus may be challenging to reach; however, it is important to try and determine what works best for different bird species in the zoo to ensure that husbandry practices remain credible.

Table 2. Potential ways for determining what flight is meaningful to an individual bird.

Measures of Meaningful Flight That Could Be Empirically Tested
The overall amount of time a bird spends in the air without interruption.
The speed that the bird can travel when performing sustained flight.
If performing flight has a positive impact on a bird’s body condition and physical health (e.g., increased musculature, improved plumage condition).
The bird’s behavioural expression (their body language) indicates positive engagement with the environment before and after flight.
Whether the bird can use sustained flapping flight to move between different enclosure areas or resources.
Whether the bird can travel between different areas of the enclosure by using different styles of flight (flapping flight, gliding).
If the bird can gain height and sustain flight at height rather than simply flapping up to a perch or descending to the ground.
How often the bird utilises resources that can only be reached by flying (e.g., perching at the tops of trees or nesting platform suspended from the ground).
Travel to, between, within, and across resources that are provided within different areas of the enclosure.
The size, shape, and location of take-off and landing points that would facilitate a bird becoming airborne and moving to different resources within an aviary.
Impacts of airflow (e.g., from life support systems) that may discourage or encourage flight and that may be particularly impactful for birds living in indoor, climate-controlled aviaries.

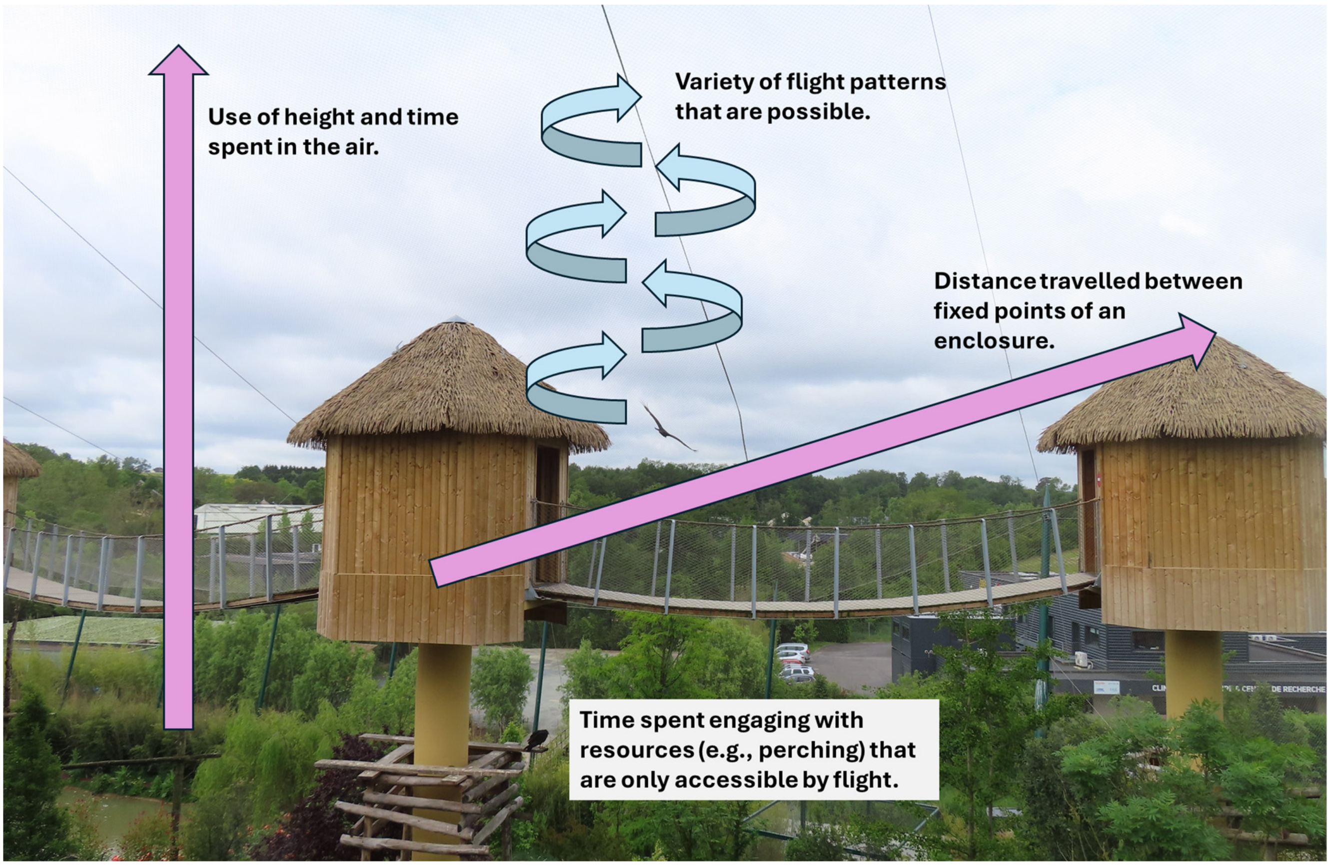

Figure 2. Potential ways of measuring meaningful flight within an aviary to understand the behavioural benefits of aviary design.

Alongside describing and measuring meaningful flight, future research should aim to identify and quantify how flight benefits captive birds. A mixture of approaches could be used, including fundamental behavioural analysis of state and event behaviours [46] to understand time-activity and the context behind them, Qualitative Behavioural Assessment (QBA) [47] to understand bird behavioural expression before and after flight to identify positive mental experiences, and physical measures of fitness and body condition to measure and quantify improved muscle development and strength. Although QBA has been used to describe what different emotional states may look like in domestic poultry [48], birds hide signs of stress or illness, which can complicate the validation of welfare measures [49]. Consequently, researchers should attempt to combine measures and look at different individual responses to flight opportunities to provide the most robust dataset possible on how birds respond to the environment of an aviary.

Those working with flying birds in zoo bird displays or public demonstrations could add valuable evidence to our understanding of what is meaningful flight from an animal welfare perspective. However, birds that were food-restricted to encourage participation in a flying display would need to be excluded from such data collection activities as such food restriction also removes choice and control and therefore the agency of the bird to fly or not. Training a bird to recognise and learn two different stimuli that represent different valences (positive—less positive) and then testing how the bird responds to a neutral stimulus after flying would enable interpretation of the judgement (pleasant, unpleasant) of flight by the bird. If birds enjoyed participating in a flying display it would be expected that they would present a more positive outlook to any such judgement bias testing. Given the evidence of how important free-flight training is to the development of adaptive behaviour patterns [25], more research into the value of training that involves flying and how birds benefit from this should be conducted across species.

As zoos are now conducting regular, individual animal welfare assessments [50], and individual animal training has become more prevalent within zoo collections, such testing of bird emotional outputs could be included as part of this welfare assessment protocol. However, significant investment may be needed in training the bird to differentiate between extreme stimuli before being presented with neutral stimuli to ensure the validity of outputs from such assessment. Zoos should also consider when a bird does not want to fly so that outward identifiers and environmental variables associated with a lack of desire to fly can be recorded and the bird's wants and needs managed accordingly.

Understanding the motivational reasons for flight, which will be based on the ecology of that species and how flight enables a bird to fit within each niche is an excellent starting point for developing species-relevant training plans, welfare assessment, or overall aviary design. A main evolutionary driver of flying style and wing anatomy is body mass [51], which is associated with how and where a species will forage within its environment [51,52] we have considered the priorities for four categories of foraging style (terrestrial feeding, arboreal feeding, aerial feeding, and aquatic feeding) in Table 3 and we pose research questions that could be implemented to gather evidence on the suitability of aviary design to meet the ecological needs of these types of birds.

The information gleaned from the questions outlined in Table 3 may help aviary designers, animal trainers, and those conducting bird welfare assessments to better tailor key elements of husbandry and management to the needs of the birds in their care. This would be particularly important when zoos are looking to move their bird collection away from a flight-restrained or flight-restricted manner of housing, into larger (potentially multi-species) aviaries that would need to have a diverse array of habitat areas recreated to ensure all species housed within such spaces can thrive.

Table 3. An example of how a bird's ecological characteristics (in this case, foraging strategy) could be used to prioritise key aspects of aviary design that could in turn be evaluated using the examples of research questions to evidence the suitability of housing for birds of this nature.

Feeding Ecology	**Provisional Priorities to Meet This Ecology**	**Research Areas to Address Such Priorities under Captive Conditions**
Ground feeding	Opportunities for scratching, digging, and turning over leaf-litter, soil, or sand. Mainly terrestrial movement but with a need to fly to escape danger or retreat when needed.	Size of terrestrial area provided and diversity of behavioural outputs. Diversity of substrate provided, and amount of time spent on exploration and active behaviours. Use of open and covered areas with an aviary to gather evidence for optimal habitat creation.
Arboreal feeding	Opportunities for searching for food on or under bark, on branches, and on and between leaves. Opportunities for climbing and movement between trees, branches, and perching. Flight between vegetation and perching for foraging, socialising and nesting.	Time spent exploring aviary planted areas (trees, shrubs etc.) and use of resources in such areas. Diversity of arboreal resources provided and any correlation with time spent on flying and exploration. Number of flights taken between foraging sites. Diversity of exploration and foraging behaviours around different planted locations of the aviary.
Aerial feeding	Opportunities for travel between feeding areas, catching and processing food on the wing, hanging or holding position in the air to forage for food. Opportunities for utilising a "sit and wait" hunting style before selecting and processing food. Flight may be utilised for specific types of behaviour at specific times of the day.	Scoring of the amount of flapping flight that is used in directional movement within an aviary. Amount of time spent flying in open space within an aviary. Diversity of food seeking, foraging, and food processing behaviour performed (on the wing or at a perch). Location and usage of perching for scanning the environment for potential food resources. Time spent on the wing for species that glide, hover, or hawk for their food. Scoring of agility and range of movements when flying.
Aquatic feeding	Opportunities for diving, plunging, swimming when foraging. Opportunities to feed on, under, or in the water and to travel/fly between different foraging patches. Flight may be utilised to travel between different foraging locations, or wings may be used on or under water or to assist with food capture (e.g., shading of a fishing site in some species of heron).	Diversity of foraging behaviour performed in aquatic areas of an aviary. Amount of time spent in aquatic habitat areas and documentation of the specific behaviours that occur. Time spent on movement between key resource areas (e.g., loafing and feeding sites). Scoring of plumage quality and condition based on amount of time spent in water.

4. Discussion

This article provides a commentary on considerations around enclosure style, amount of space, and the promotion of bird flight to uphold a good animal welfare state, enhance the conservation relevance of avian populations, and ensure better husbandry practice moving forward. Practical aviary design and construction has long considered bird health as a primary driver, such as increasing survival rates by reducing pathogen accumulation and prevalence of disease [53] but, as zoos move forward with greater consideration of psychological wellbeing, the protection of behavioural repertoires and emotional states also needs equal consideration to biosecurity.

Play has been observed in various species of bird when in flight [54] and this evidences that birds fly for more than the simple reason to travel from one location to another. Identification of different reasons for flight would allow aviary designers to include environmental resources of different sizes, styles, or accessibility (perhaps that can be accessed at different times of the year) to ensure that the fullest behavioural repertoires possible can be expressed. As species that play are often those of higher cognitive ability or with a delayed maturation phase [54], consideration of how a bird develops behaviours via interaction with their social and physical environment should also be a key consideration for enclosure designers. Such questions could be the following: How much space does an individual need to play with their conspecifics?; Where does play occur—in what dimension of an enclosure?; how fast do birds fly when playing, and where do resources need to be located to reduce collision? Aviaries designed for non-breeding, juvenile birds may need to be of a different design, with different amounts of space for flight, play, and socialising, compared to that provided for breeding adult birds. Such behavioural-specific aviaries could encourage the development of social bonds that facilitate mate choice and compatibility, which would eventually promote sustainable ex situ populations.

We could consider the previously mentioned Tinbergian approach to unpick the effect of different situations that a species is housed in and what the result of a lack of flight, or promotion of flight may be to the population in the zoo overall. Figure 3 suggests a Tinbergian framework in the manner of Mellor et al. [28] for assessing improvements to behaviour and welfare for birds that are commonly housed in a flight-restricted manner (e.g., feather-trimmed or in aviaries of a size that do not allow for meaningful flight), in this case, Marabou (*Leptoptilos crumenifer*). Opportunities for flight may enhance engagement with causal factors for a wider range of behaviours because birds can explore different resources or enclosure dimensions when flying. Birds will also develop physically when flight is possible and this may impact their abilities to perform other behaviours in a more species-typical manner. As changes to bird morphology can occur that are suggestive of adaptation to captivity [55], enhancing abilities to fly (such as by providing more space via the construction of larger aviaries) can ensure that wild traits are conserved in ex situ populations. Alongside this, consideration should then be given to the style and structure of perching within an aviary. Birds that are travelling for longer times in the air may require perches of different flexibility than when housed in aviaries where the bird is airborne for much shorter periods of time. As the style of perching (its diameter, uniformity, rigidity, and location) will impact bird foot health [56], perches may need to become more species-specific as aviary design enables more opportunities for prolonged flight.

There is evidence that welfare is not compromised by flight restraint for some captive species when measured using comparative behavioural approaches [57] and physiological indicators [58,59]. Consequently, data need to be collected across facilities to fully understand how individuals within a species respond to different forms of enclosure (covered aviary or open-topped) as well as shape and size (length, height). As different populations of the same species of bird can show behavioural flexibility based on environmental challenges, e.g., different organisation of migration affectivity by whooper swans that breed at higher or lower altitudes [60], it is important to consider the origin of bird populations in zoos and what challenges they may be capable of adapting to or coping with. This may, in turn, have an impact on the amount of flight seen in zoo housing. Figure 4 provides a schematic representation of how research questions could be implemented to collect such comparative data.

Those who are designing and building housing for birds in human care need reliable and robust information on the following metrics to ensure that such housing is future-proofed and supportive of maintaining a sustainable population for the future. A systematic review of the literature can provide data on the behavioural diversity of free-living bird species that is then helpful for evaluating captive activity patterns [35]. Direct observation of free-living individuals can also be undertaken to further decipher how a species partitions time within specific elements of its time budget [61]. Behaviours such as travel time in the wild may be useful indicators of how important flight is, and what space is provided in the zoo. Instead of post-occupancy evaluation zoo enclosure designers could use a pre-occupancy modelling method based on similar modelling methods used in ecology [62], for example using calculations of wild travel time and distance along biologically relevant habitat areas to construct an aviary of a shape and size that enables flight over similar times and distances. Long-ranging movement patterns can be simulated in the zoo, as has been demonstrated by research on zoo-housed elephants (Elephantidae) that shows parity between wild and zoo animals in terms of daily walking distance [63], and therefore creativity in aviary design and furnishing could bring similar behavioural benefits to captive birds.

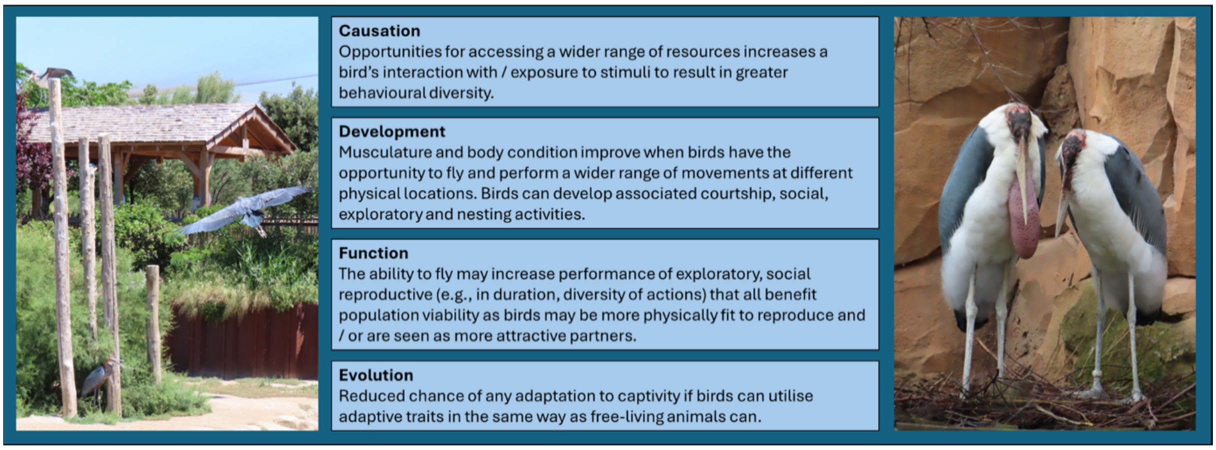

Figure 3. Potential application of Tinbergen's Four Questions to our understanding of the positive behavioural and welfare benefits of enabling bird flight in species that may traditionally be kept flight-restricted, to enhance individual bird behavioural diversity and quality of life, and to improve the sustainability and conservation relevance of the population.

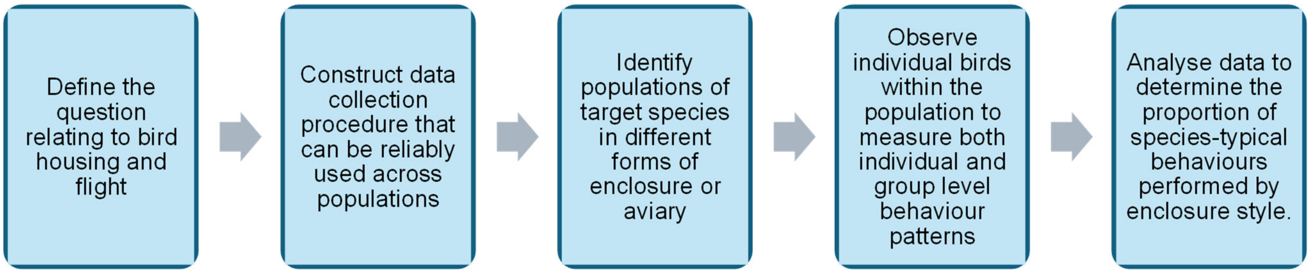

Figure 4. A potential strategy for evidence gathering to understand any impacts of housing on bird flight.

Mellor et al. [64] pose a hypothetical example of daily travel time as a potential predictor of negative welfare indicators in the zoo (e.g., the proportion of time spent on stereotypic behaviour patterns), with the need to consider species evolutionary relatedness (phylogeny) when comparing datasets. The idea behind Mellor et al. [64]'s example is that bird species that are more aerial in the wild are more likely to suffer compromised welfare in an enclosure compared to species that spend more time being terrestrial. Taking this hypothetical example and adding actual data to it, whilst using phylogenetic comparative approaches to control for evolutionary relatedness would help us to determine the earlier question of "What is meaningful flight?" and provide answers to questions around how flight restraint impacts bird's physical health and behavioural and psychological welfare. It may also be important to consider the other evolutionary and ecological factors that predispose a bird to perform either a specific behaviour or succumb to a welfare challenge, as Mellor et al. [65] identify the multifactorial influences that predispose some species of parrot (Psittaciformes) to poorer welfare when housed under human care.

Changes to bird housing in zoos may result from biosecurity needs and prevention of future disease outbreaks, such as the need to reduce the probability of cases of the highly pathogenic Avian Influenza [66]. Pressures to move birds from open enclosures to covered housing to lower any risk of emerging disease outbreaks and preserve zoo operations means that a focus on appropriate aviary design continues to be important. For species that may not have been traditionally kept in aviaries, evidence gathering is required to ensure that any new housing provides the same behavioural benefits as larger, open-topped exhibits.

It is essential that birds housed in large aviaries, which promote meaningful flight, can be reliably and accurately managed. Providing more space does not mean that welfare will automatically be good, as welfare is a continuum that changes over time [67], and keepers need to be able to take records of the animals they are caring for. This means that the population of each species in an aviary needs to be counted and observed daily. In spacious, naturalistic aviaries, birds will need to be trained to enable catching and handling when required. A key welfare concern of large, multi-species aviaries may be the lack of individual animal management or the chances of finding sick or injured individuals. Good animal management regimes are essential to protect and uphold the welfare of all individual birds in housing styles that are naturalistic, have multiple habitat areas, and contain a large number of individual birds. Zoos should collaborate to share ideas on how good population management in a large aviary can also mean that individual bird management is also realised.

Such collaboration also needs to extend to off-show areas and indoor housing. Whilst some constraints and more restricted housing may be required (e.g., for veterinary procedures, to facilitate moves to other organisations, or to simply provide warmer shelter from inclement weather), indoor housing metrics also need evidence. What is the measure of useful space for a bird housed indoors? Is this based on wing length? Or should this be considered on the amount of movement that the bird seeks to perform, along their perching or in the air? The same considerations may be needed for breeding aviaries, compared to display exhibits for non-breeding flocks. Further focus on space that birds need when housed indoors is vital to protect well-being, particularly when individuals are not housed "on exhibit", and to ensure that all highly motivated behaviours can still be performed as and when needed.

It is also important that the needs of birds without a reliance on flight are not forgotten. Providing resources that allow for camouflage or background matching, ensuring thick patches of vegetation are provided in different enclosure areas for species that skulk away or hide when threatened, and ensuring that aquatic species can take to the water and swim or dive when needed, are all just as important as enabling flight. The key to success for the aviary of the future is to allow all bird species housed within the chance to fly, should they want to, whilst allowing for their preferred mode of locomotion and resource access (Figure 5). Therefore, valid measures of space usage [68,69] should be employed to assess how much time birds spend engaging with specific resources, as such data will provide evidence for how to develop habitat features within an aviary to ensure the environment is suitable for all species being housed. Such considerations carry greater relevance as zoos are moving towards the creation of more mixed species aviaries; therefore, the needs of all bird species have to be catered for within the same exhibit space [70,71].

A further requirement of the "future aviary" is that it must be adaptable. Rarely can zoos afford to rebuild an existing enclosure to accommodate a new species, and to encourage sustainability and reduced carbon footprints, zoos must consider the refurbishment, regeneration, and reconfiguration of enclosures as collections change. Ultimately, an aviary must be simultaneously generic and specific. The physical structure of an aviary, regarding its dimensions and mesh size, may be required to contain birds as diverse as small Passeriformes, to ground-dwelling Galliformes, to New World vultures (Cathartidae) so it is the interior furnishings that must be managed, created, and then adapted for the needs of each species. Hopefully, such an approach would encourage aviary designers to "think bigger" from the first concepts of the aviary rather than creating something inflexible that may, in the longer term, take more time, effort, and resources to adapt and evolve (alongside changes to better practice husbandry and desired welfare outputs). We encourage more zoo designers and zoo biologists to collaborate further on this, to ensure that aviaries can provide for current species and those that may come into human care in the future. Such collaboration will be particularly important to ensure that birds do not injure or harm themselves when they fly within their aviary. Mesh design, the placement of structural supports, and the layout and placement of aviary furnishings all need to be considered so that if birds can fly, and fly long distances within an aviary, they are able to navigate, take off, and land safely at all times. Therefore, zoo designers, biologists, animal care staff, and veterinary surgeons need to integrate information on flight speed, manoeuvrability, take-off routes, and space needed for landing into how an aviary is designed, built, and furnished to cater for the flight movements of all species housed.

Figure 5. Enabling flight and opportunities to access resources that can only be accessed by flight in species where other modes of travel might be considered more important. Left: Speckled Teal (*Anas flavirostris*) perching on high trunks and a cliff edge. Whilst appearing unusual for a species of waterfowl, birds will access such resources when given the choice. Centre: Yellow-necked Francolin (*Pternistis leucoscepus*) climbing over a cliff face that involved flapping flight to access. The bird's cryptic plumage camouflages them against a similar coloured backdrop and therefore by matching the environment to the bird's ecology, the animals feel comfortable using a wider range of enclosure areas. Right: canopy usage by a Great Blue Turaco (*Corythaeola cristata*) and a Yellow-billed Stork (*Mycteria ibis*). The forest-dwelling turaco that jumps and clambers between branches has the option to fly between trees to use all dimensions of perching and cover provided by mature trees. A Yellow-billed Stork, a wetland species, can utilise the tree canopy for nesting without disturbing the activity of forest-dwelling species, such as the Great Blue Turaco.

Understanding which restrictions from the wild can be built into an enclosure (in a manageable and non-dangerous way) could present birds with new challenges that enhance behavioural outputs. For example, aviaries that provide a wide variety of social interactions yet allow space to move away from conspecifics when desired would enhance behavioural diversity and give birds the opportunity to utilise different forms of flight for different reasons. The same would be true for aviaries that recreate different habitat areas where birds can congregate, encounter competition, yet move to another (equally valued) area when they choose. Zoo designers should consider recreating habitats within areas that keep territorial species separate or colony nesters together without the need for physical barriers. Eustress (i.e., positive challenge) is beneficial to positive welfare states and builds an individual's resilience that buffers against stress [72]. Such positive challenges would be the result of birds having opportunities to fly and then access different habitat areas, different resources, and engage with conspecifics and social interactions with other species. This resilience would be essential to the wider relevance of ex situ bird populations to conservation actions (i.e., they would display wild-type behaviour patterns and develop behaviours suitable for survival in a dynamic environment) and, therefore, cement the role of zoo-housed individuals to One Plan Approaches to Conservation [73] that seek to integrate ex situ and in situ populations within wider conservation aims.

Finally, as aviaries become larger and more species of bird are provided with the opportunities to fly, it may be important to consider new behavioural indicators of poor welfare that are expressed when flying. Such abnormal repetitive activities would have been unable to be performed in more flight-restrictive conditions but could manifest as route tracing and other invariant movements within the flight space of an aviary, which may have a similar causation to the locomotory abnormal repetitive behaviours seen in other species of zoo-housed mammals [74,75], herptiles [76], and fish [77]. Ensuring the quantity of space provided is of good quality to promote behaviours that are relevant to the individual may be one way of ensuring that such stereotypic activities do not persistently develop in flighted birds in large, expansive aviaries.

5. Conclusions

Flight is a common behaviour for the majority of birds, and the goal of this manuscript was to evaluate how any need to fly is considered and integrated into bird husbandry and management (specifically concerning aviary design). Enclosure design needs to consider this characteristic of birds and ensure it can be meaningfully provided for based on the species being housed. The zoo of the future needs to design and build enclosures that ensure population sustainability. An evidence-based approach is essential to all aspects of zoo operations, especially those focused on animal management. Zoo organisations are collaborating to develop approaches to enhance husbandry that will be the foundation for housing and enclosure design over the next few decades. As such, these important documents need to detail optimal approaches to how species should be housed to maximise the display of natural behaviour, protect and promote animal welfare and population sustainability, and reduce any effects of artificial selection. We need to collect more evidence on what housing and husbandry practices are best to ensure that birds can function appropriately. Although zoos are striving towards the measurement of the fifth domain for their animals, if care is not correct for that species, the animal will never achieve positive mental outputs. We are therefore focusing on the wrong element of welfare and, as such, bird husbandry guidelines must continue to seek evidence as to what form of housing and enclosure style promotes the best welfare outputs. A relabelling of best practice approaches to husbandry as "better practice approaches" would rationalise the need for housing and husbandry to be continuously reviewed, evaluated, and reassessed so that they continue to develop alongside our understanding of what animals need from their environments and from their care. Finally, zoos should consider which welfare compromises the public is going to tolerate moving forward. Birds have evolved to fly, and we must question if flight restraint is something that can morally or ethically continue, even if open-topped enclosures for feather-trimmed individuals provide space and opportunities for behavioural diversity. The zoo community, plus those in the field of designing and constructing aviaries, should extend dialogue and discussion and get more creative in the scope and scale of enclosure design for the future so that as many zoo-housed birds as possible can experience the wider behavioural benefits of flight and any associated health and welfare enhancements.

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