# Overview

# A Bird's-Eye View of Regulatory, Animal Care, and Training Considerations Regarding Avian Flight Research

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A thorough understanding of how animals fly is a central goal of many scientific disciplines. Birds are a commonly used model organism for flight research. The success of this model requires studying healthy and naturally flying birds in a laboratory setting. This use of a nontraditional laboratory animal species presents unique challenges to animal care staff and researchers alike. Here we review regulatory, animal care, and training considerations associated with avian flight research.

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From Greek mythology to Da Vinci's works on the flying machine, the flight of birds has fascinated men. The modern-day study of flight is central to many disciplines: ecologists study flight to better understand the evolution and preservation of a species; biologists seek to understand how different organ systems interact to achieve flight; physicists aim to model the physical properties of flight; and engineers seek to apply these findings to facilitate advances in aviation and the design and control microaerial vehicle. The use of birds to further our understanding of flight is essential to each of these endeavors. Although noteworthy advances have been made in our understanding of the mechanisms mediating flight,74 many questions remain to be answered.<sup>39-41,73</sup> Furthering our understanding of flight often requires studying flying animals, typically birds, in a laboratory setting. This need presents unique challenges to veterinary staff, IACUC, and researchers alike. This review examines some of the challenges posed by avian research and summarizes regulatory, animal care, and training considerations associated with this important field of research.

# **Regulatory Oversight of Avian Flight Research**

Together with laboratory rats and mice, birds are specifically excluded from the Animal Welfare Act.<sup>1</sup> The federal regulation of ornithological research stems from the Health Research Extension Act of 1985.<sup>26</sup> Under this Act the then-director of the NIH established the Public Health Service Policy,<sup>57</sup> which pertains to all live vertebrate animals used or intended for use in research, research testing, experimentation, or biologic testing or related purposes and mandates the adherence to the *Guide for the Care and Use of Laboratory Animals*<sup>29</sup> (the *Guide*). Compliance with these regulations is required if an institution intends to conduct animal activities supported by the Public Health Service, National Science Foundation, Department of Defense,

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or Veterans Affairs or if an institution is to become AAALAC-accredited.

At the institutional level, IACUC are tasked with overseeing the animal program, facilities, and procedures to ensure that they are in compliance with applicable regulations (Public Health Service Policy, the Guide, Guide for the Care and Use of Agricultural Animals in Research and Teaching,<sup>21</sup> and the Animal Welfare Act Regulations,<sup>2</sup> insofar as these may apply). Among other responsibilities, the IACUC reviews all proposed study activities prior to initiation to ensure that procedures will avoid or minimize pain and distress to the animals through rigorous design and the provision of appropriate sedation, anesthesia, analgesia, and euthanasia. In addition, IACUC should ensure that the living conditions and program of animal care is appropriate for the avian species to be housed. As with previous overviews for other avian research models,<sup>67</sup> the current review should serve as an aid to IACUC or veterinary teams when avian flight research is being established in a facility or when reviewing proposed avian flight research studies.

### **Field Studies**

Field studies are commonplace in avian flight research, because they allow for observations and measurements of a range of flight behaviors that may be impossible or impractical in a research facility. At a minimum, IACUC must be provided with the location of the intended field study, the proposed procedures, and a description of how these procedures might affect the biology and ecology of the studied animals and others in the immediate study area. In addition, IACUC must be provided with assurance that permit requirements of pertinent local, state, national, and international wildlife regulators will be met before work begins. At this point, if the IACUC determines that the proposed activity will not alter or influence the study animals or their environment, then further review is not needed. However, if the IACUC determines otherwise, then full protocol review and subsequent approval is required before initiation of the study. For avian field studies, semiannual IACUC inspections of study sites are not required and often are

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impractical; however the circumstances should be explained to the IACUC so that they can consider risks to personnel and effects on study subjects. This notification may be partially accomplished through written descriptions, photographs, or videos that document the study site. The increasing availability of video calling, even in remote or inaccessible areas, has the advantage of allowing real-time interaction and engagement of the researchers at field sites with local IACUC and veterinary personnel. This technology enhances the review process beyond that which might be achieved through photos and written reports. Additional details on the review of field studies can be found in a number of IACUC books,<sup>24,69</sup> the *Guidelines to the Use of Wild Birds in Research*,<sup>20</sup> and the NIH Office of Laboratory Animal Welfare website, specifically the Frequently Asked Questions.<sup>58</sup>

#### **Obtaining Birds for Use in Flight Research**

Although field studies accommodate observations and recordings of flight in a bird's natural habitat, flight research often requires studying birds in a more controlled, laboratory setting. However, procuring birds can be a challenge for researchers. The species of bird selected by the researcher depends on a combination of practical considerations, including the size of the bird (smaller birds are obviously advantageous for maintaining in the laboratory setting) and plumage coloring (for example, birds with certain shades of colors may be preferred against a particular background for image contrast enhancement), and the type of flight being studied. In particular, different birds have different patterns of flight-from specialists, such as the hummingbird, to generalist fliers. Smaller generalist fliers may display typical flap-glide-bound pattern of flight,<sup>65,75</sup> whereas birds heavier than approximately 300 g flap continuously.<sup>76</sup> In addition, flying birds can be grouped broadly into categories based on wing tip shape (rounded, pointed, convex or concave) as well as the aspect ratio of the wing (stubby or slender).<sup>44</sup> Bird species used in flight research include, for example, pigeons,<sup>81</sup> hummingbirds,<sup>83</sup> quail,<sup>3</sup> zebra finches,<sup>77</sup> starlings,<sup>9</sup> corvids,<sup>30</sup> cockatiels,<sup>28</sup> lovebirds,<sup>37</sup> parrotlets,<sup>14</sup> chukar partridge,<sup>7</sup> turkeys,<sup>64</sup> seabirds,<sup>62</sup> hawks,<sup>79</sup> and eagles.<sup>10</sup> Regardless of the model chosen, none of the species of birds just listed are purpose-bred for research; consequently high-quality SPF sources are not readily available. Researchers are therefore often forced to obtain birds from private breeders, such that birds can vary dramatically in both the quality and consistency of their health and genetics. This situation can have adverse effects both on research replicability and on the health of both individual birds and the colony as a whole. In addition, many private breeders may be reluctant to sell birds to be used in research, especially research that may be invasive or terminal in nature. Establishing a long-term relationship among researchers, veterinarian, and breeders may help to mitigating these issues.

As an alternative, birds can be wild-caught, but this practice also is not without its challenges. Obtaining the appropriate permits for wild capture is time-consuming and can be arduous, particularly when the target species is either rare or considered an invasive species, because invasive species cannot be released once caught. Capturing birds can be technically challenging, necessitating experience and training, of which the IACUC should be informed. In addition, the capture process can potentially expose researchers to members of the public, particularly in more urban areas. Therefore, consultation with the institution's public relations office should be considered during the protocol review process when wild capture is pursued. Furthermore, obtaining birds from the wild may have occupational health and safety concerns, both from injury and risk of zoonotic exposure. Researchers should therefore be made aware of these risks and work with the IACUC throughout protocol review to ensure that appropriate steps to mitigate these risks are taken. Biosecurity implications should be factored in when wild-caught birds are brought into a facility, due to the risk of within-species and cross-species disease transmission. Acclimation of wild birds to captivity can be a major issue, and a prolonged period of quarantine and steady acclimation along with appropriate preventative veterinary care—is necessary to avoid significant loss of life that can occur during this time. Even with a successful acclimation period, wild-caught birds are harder to train than their domestic counterparts, thus potentially greatly extending the time required to complete an experiment.

#### Housing

The incredible diversity of birds studied in flight research, from the 4-g Anna's hummingbird<sup>38</sup> to the 4-kg steppe eagle,<sup>63</sup> proves an obvious challenge for the animal care team when considering housing. Special attention must be paid to the details of the housing set-up, because poorly designed housing can have negative effects on both research and the welfare of the birds. In general, evidence-based minimal space requirements for avian species are sparse, although some guidelines have been established in the United States and Europe (Figure 1). However, these minimal guidelines often are not followed.<sup>4</sup> In addition, general husbandry guidelines have been published for some avian species.<sup>8,33</sup> For avian species where space allowances have not been established, birds must at least have enough space to hop and fly between resting (for example, perch) and feeding areas in the cage, using fully extended wings that do not touch the side walls. Smaller cages can elicit abnormal behaviors,<sup>5,22</sup> such as increased stereotypies and decreased time spent on cage-floor foraging. The length of the enclosure is a particularly important consideration for birds used in flight research, because they need to be able to achieve flight outside of the take-off and landing phase to allow for the correct development and maintenance of flight musculature for study. In addition, longer cages have been associated with fewer stereotypies than taller or shorter cages in some species.<sup>5</sup> The height of the enclosure should be considered also, so that social species can express dominance hierarchies and to allow prey species the feeling of being able to escape human 'predators' by positioning themselves above them.11 When birds are habituated to humans and are used to receiving food rewards, it is important to provide perches both in the back of the cage and near the cage door, so that birds can approach humans at their own pace for receiving food.

Beyond housing, enrichment programs are an essential component of the animal care program for birds. Enrichment programs can be inspired by the natural history of the species, in particular in relation to foraging, social, and resting behaviors. Ideally, these programs should aim to be evidence-based in their nature and designed to increase the range and duration of expression of species-specific behaviors. To this end, they should be reviewed periodically to ensure that these aims are being achieved and in a cost-effective manner. As a minimum, birds should be provided with perches because, in general, they prefer to remain elevated from the ground. In addition, nest boxes and nesting material should be provided for some species and are necessary for breeding. In addition, other enrichment devices, such as mirrors, which have been shown to be beneficial, may be placed in the enclosure.<sup>45</sup> In general, birds

Species	Weight	Floor space	Cage height
African gray parrot, <i>Psittacus erithacus</i> <sup>25</sup>	Average weight, 400 g	Cage length of 9.8 ft (3.0m) per	
	Average length, 33 cm	pair of birds	
Budgerigar, Melopsittacus undulatus <sup>25</sup>	Average weight, 29 g	Cage length of 1.6 ft (0.5 m) per 1	
	Average length, 18 cm	pair of birds, add 1.6 ft (0.5 m) for	
		each additional pair	
Chicken, Gallus domesticus <sup>29</sup>	<0.25 kg	0.3 ft <sup>2</sup> (0.02 m <sup>2</sup> )	Cage height should be
	<0.5 kg	0.5 ft <sup>2</sup> (0.05 m <sup>2</sup> )	sufficient for the
	<1.5 kg	1.0 ft <sup>2</sup> (0.09 m <sup>2</sup> )	animals to comfortably
	<3.0 kg	2.0 ft <sup>2</sup> (0.19 m <sup>2</sup> )	stand erect, with their
	3.0 kg and larger	≥3.0 ft <sup>2</sup> (≥0.28 m <sup>2</sup> )	feet on the floor
Cockatoo (for example, white-crested	Average weight, 440 g	Cage length of 23 ft (7.0 m) for a	
cockatoo, <i>Cacatua alba</i> <sup>25</sup> )	Average length, 46 cm	single animal or 1 pair of birds	
Lories and lorikeets (for example,	Average weight, 130 g	Cage length of 3.9 ft (1.2m) for 1	
green-naped lorikeet, Trichoglossus	Average length, 27 cm	pair of birds, add 2.0 ft (0.6 m) for	
haematodus <sup>25</sup> )		each additional pair	
Lovebirds (for example, peach-faced	Average weight, 55 g	Cage length of 3.9 ft (1.2 m) for 1	
lovebird, Agapornis roseicollis <sup>25</sup> )	Average length, 15 cm	pair of birds, add 3.3 ft (1.0 m) for	
		each additional pair	
Macaws (for example, scarlet macaw,	Average weight, 1.0 kg	Cage length of 13.1 ft (4.0 m) for 1	
Ara macao <sup>25</sup> )	Average length, 90 cm	pair of birds, or 49.2 ft (15 m)	
		when not breeding	
Parakeets (for example, Indian	Average weight, 115 g	Cage length of 9.8 ft (3.0 m) for 1	
ringneck parakeet, <i>Psittacula krameri</i> <sup>25</sup> )	Average length, 40 cm	pair of birds; addl 4.9 ft (1.5m) for	
		each additional pair	
Pigeon, Columba livia <sup>29</sup>	1 bird	0.8 ft <sup>2</sup> (0.07 m <sup>2</sup> )	
Quail, Coturnix coturnix <sup>29</sup>	1 bird	0.3 ft <sup>2</sup> (0.02 m <sup>2</sup> )	
European starling, <i>Sturnus vulgaris</i> <sup>25</sup>	1 bird	5.4 ft <sup>2</sup> (0.5 m <sup>2</sup> )	1.0 ft (0.3 m)
	<6 birds	16.1 ft <sup>2</sup> (1.5 m <sup>2</sup> )	1.6 ft (0.5 m)
	<12 birds	21.5 ft <sup>2</sup> (2.0 m <sup>2</sup> )	3.3 ft (1.0 m)
	12 birds or more	$\geq$ 32.3 ft <sup>2</sup> ( $\geq$ 3.0 m <sup>2</sup> )	5.7 ft (1.8 m)
Zebra finch, <i>Taeniopygia guttata</i> 25	1 bird	3.2 ft <sup>2</sup> (0.3 m <sup>2</sup> )	1.0 ft (0.3 m)
	Breeding pair	3.2 ft <sup>2</sup> (0.3 m <sup>2</sup> )	1.0 ft (0.3 m)
	<6 birds	6.5 ft <sup>2</sup> (0.6 m <sup>2</sup> )	1.0 ft (0.3 m)
	<12 birds	10.8 ft <sup>2</sup> (1.0 m <sup>2</sup> )	4.9 ft (1.5 m)
	12 birds or more	16.1 ft <sup>2</sup> (1.5 m <sup>2</sup> )	6.6 ft (2.0 m)

Figure 1. Space allowances for bird species commonly used in flight research. Space allowances are taken from US guidelines where available. When unavailable, European guidelines are provided.

need water baths so that they can clean and preen themselves daily, allowing maintenance of optimal feather quality. For other species, dust baths can be added to cages, either continuously or temporarily, and have been shown to be important in some species, such as quail, who will demonstrate sham dust-bathing behavior in their absence.<sup>53</sup>

When designing the enrichment program, it is important to consider species-specific preferences and normal behavioral tendencies. Although both corvids and psittacines are highly intelligent groups of birds,<sup>18</sup> in general, corvids are naturally more neophobic whereas psittacines are naturally more exploratory.<sup>6</sup> In addition, there is variation within the psittacine group, and African gray parrots can be relatively neophobic.<sup>60</sup> Therefore, although providing more exploratory species with frequently changing enrichment may be beneficial in promoting expression of behaviors, providing frequent novel items to the more neophobic species may have detrimental effects to the birds' psychologic wellbeing, thus countering the purpose of

the enrichment program. In addition, parrots have been shown to have preference for size, color, and texture of enrichment devices,<sup>35</sup> and enrichment devices have long-term effects on behavioral phenotypes.<sup>51</sup> The introduction of new items, sounds, people, and other novel experiences thus needs to occur in gradual steps, so that birds can adjust and habituate. The pace between approximations is set by the individual bird, which should not display arousal or escape behavior with each approximation. Therefore, knowing and being able to observe the behavioral tendencies of the species—and even individual birds—being housed can be very helpful for guiding the enrichment program.

Although providing enrichment is undoubtedly important to promote species-specific behaviors, it must be done in a way that is compatible with routine husbandry and project-specific scientific procedures. From the husbandry standpoint, enclosures should be designed to ensure daily provision of fresh food and water, removal of excess fecal waste, and ease of Vol 69, No 3 Comparative Medicine June 2019

health observation by the animal care team. From the researcher's standpoint, animals must be accessible for the interactions and training required to complete research goals. All parties—research, husbandry, and veterinary—must therefore be collaboratively engaged in the design of the enrichment program.

An additional and important aspect when considering the specifics of housing and enrichment programs is social housing. The Guide states that single housing of social species should be the exception, thus implying that social species should be housed in pair or group settings. Single housing of social species can be justified in light of experimental requirements or veterinary-related concerns about animal wellbeing but should be reviewed frequently by IACUC and veterinary personnel. The majority of avian species used in laboratory studies of flight are found in social groups in the wild and should therefore be group-housed. When cohoused, birds form strong pair bonds, and removing an individual animal can be stressful for both birds. In addition, studies have shown that, compared with singly housed birds, cohoused birds can learn tasks quicker than because they learn from watching their cagemate<sup>56</sup> and are more cooperative and easy to train,<sup>49</sup> if the trainer is experienced. However, training birds in social housing can be challenging for researchers. During training, the dominant bird often displaces the subordinate to gain access to food rewards. This situation can result in rewarding the incorrect behavior of the dominant bird and not rewarding the correct behavior of the subordinate bird, thus confusing and prolonging training. Therefore, it is key to organize training sessions with a single bird in a cage to train effectively. While doing so, it is important that the cages of flock mates are close enough for birds to stay in vocal contact. Visual contact during training should be controlled: whereas it is beneficial for peer-learning, it should be avoided otherwise to prevent birds from attempting to fly over to other cages during training sessions.

One particular challenge for social housing is pair bonding, because some species do not bond well unless birds are placed together when they are still juveniles, and it can be even harder if they have been pair-bonded with other mates before. Another challenge can be pair housing of sexually mature male birds, which can lead to fighting, particularly during the breeding season. Beyond the negative welfare implications, fighting may lead to damage to feathers or wing structures, which may temporarily or permanently affect their ability to fly optimally and thus adversely affecting research goals. Any bird that does require single housing should, at a minimum, be housed with visual and auditory access to compatible conspecifics, and ideally cages should be designed to allow preening between single-housed birds. This access should be achieved in a stepwise manner, where the cages are initially placed adjacent and the birds are observed to ensure absence of aggressive interactions. This aggression can be an issue with wild-caught, male pairings, especially in breeding season. If positive interactions are noted at this stage, cages can be pushed together to allow for direct contact, with follow-up monitoring of birds for signs of fighting. This degree of contact is especially important in species that depend on social preening (allopreening) for removing pinfeathers from their heads and for social bonding, such as parrots.<sup>68</sup> Decisions on appropriate social housing should therefore be carefully considered to optimize both animal welfare and research outcomes.

#### **Positive Reinforcement Training**

The cooperative training of birds is essential for many forms of flight research. Birds must be trained to fly between 2 points for almost all types of flight studies, including wind-tunnel experiments,19 force-plate analysis,42 and video analysis.63,71 This training is challenging, because birds must overcome their natural fear of humans, who may be viewed as predators, depending on their natural history and previous experiences. This fear can be especially strong in wild-caught birds. Overcoming the fear of humans requires that all interactions-whether related to husbandry, veterinary, or research activities-be conducted in a way that results whenever possible in a positive experience for the bird and requires habituating the bird to new experiences through approximate steps. Therefore, training through positive reinforcement is essential; otherwise, the research will be limited to studying human-induced escape behaviors.<sup>30</sup> Not only do escape behaviors only represent a small part of a bird's natural behavior repertoire, birds can quickly habituate, thus limiting the number of trials. The outcome from escape compared with natural foraging behaviors can be very different. Birds foraging between perches based on rewards choose take-off angles that minimize foraging energy expenditure,<sup>14</sup> whereas birds escaping take-off over a more erratic range of angles. Furthermore, in muscle physiology studies, incomplete recovery after invasive procedures alters wing kinematics and overall flight behavior.78 Ensuring minimally invasive procedures with full recovery and training based on positive reinforcement are key enablers for studying the natural low-stress behaviors birds display during most of their lifetime. Therefore, because of the importance of positive reinforcement training, facility design, the enclosure, and husbandry, veterinary, and research practices must all be optimized to help achieve this goal.

Loud noises can evoke marked startle responses in birds. Birds should therefore be housed away from high-traffic and high-noise areas such as cage wash, auditory alarms, and loud species such as pigs and dogs. However, it is not possible to completely remove all auditory disturbances. To address this problem, lower decibel level versions of the sounds that the birds will experience throughout housing and experiments can be played in their aviary space to habituate them. Example of sounds that can be played include knocking on and shutting doors, manipulating research and husbandry equipment, and sounds made by research equipment such as fan noise from wind tunnels. Podcasts can be played to accustom the birds to a variety of voices. However, the use of generalized noise across a broad band with a decibel level that masks vocalizations of flock mates should be avoided at all time in the husbandry space, because it has been shown to be an effective bird deterrent.<sup>46,72</sup> Caging, transport, and research equipment should be designed so that tasks can be performed with minimal stress to birds. For example, cages can be designed to allow for easy transfer of birds during routine cage change sanitation, and birds can be trained through positive reinforcement target training to fly from one to the other. Finally, it is essential that all personnel handling the birds be trained in reading both normal behavior and behavior associated with fear and stress so that personnel can identify and subsequently reduce the number of fearful and antagonistic interactions that birds experience.

With new birds, the number of new people that enter the room, and variations to the daily schedule, should initially be minimized to allow for gradual habituation to people and routines. Routine veterinary procedures that involve the capture and restraint of the birds can be particularly stressful. Disassociating these procedures from the people conducting them is important for continued trust and stress-free behavior from the birds. It is essential to maintain the bird's eagerness to train. This attitude can be achieved by performing capture and examinations in the dark by using night-vision goggles (for example, using infrared lights to illuminate the room and having the handler wear virtual reality goggles with an infrared-sensitive camera attached [Figure 2]) or by using specially designed hoods or blindfolds on the birds. Although these measures can be cumbersome and take a while for the bird handler to get used to, they can be very effective, allowing for successful completion of veterinary procedures while minimizing the stress on the birds. Taking this accommodation one step further, it has been shown that birds can be trained to voluntarily participate in veterinary procedures.<sup>16,47</sup> Only by minimizing stress and using positive reinforcement training will birds cooperate voluntarily and therefore consistently fly in the most natural manner. This approach is particularly effective when the caretakers frequently train the necessary behaviors.

Positive reinforcement training by caretakers and researchers requires habituation to hand feeding to be successful (Figure 3). This goal is easiest to accomplish in birds that have been bred for this specific purpose and in which hand feeding was introduced at an earlier age. However, other birds, including wild caught, can be habituated to hand feeding. The time to successfully habituate to hand feeding typically is longer for wild-caught birds, especially those that interact with humans in way that has made them cautious of our presence, than purpose-bred birds. Therefore, researchers should assess how much time they are willing to invest toward taming and obtain their birds appropriately. Alternatively, wild birds can be trained with automated feeders to perform simple behaviors without people present; however, this situation limits the usefulness of this approach in research and requires customized engineering to accommodate species-specific morphology and behavior. Examples of positive reinforcement training are shown in Figures 3 through 5. These figures outline the necessary steps to train a variety of behaviors that are particularly useful for flight research and that can be implemented for many bird species. For further understanding of the principles of positive reinforcement training, excellent texts have been written for veterinarians<sup>61</sup> and researchers<sup>48</sup> to review.

The time required to successfully train new behaviors depends not only on the species involved but also depends on the capability of the trainer. An experienced trainer can teach a new behavior with just a few well-planned cue-reward pairs over a small number of training sessions. A novice trainer may need many training sessions over the course of multiple days to accomplish the same training. This prolonged time could be due to reinforcement of incorrect behaviors, inaccurate bridge timing, or poor decision-making regarding the intermediate steps to reward. Those new to training birds should first observe only and then work in tandem with experienced bird trainers, before finally being allowed to work alone. In an ongoing effort to improve training effectiveness, the person training the bird can periodically film their training sessions with both trainer and bird in view and then can analyze a randomly selected video clip with coworkers to get feedback.

#### **Veterinary Care**

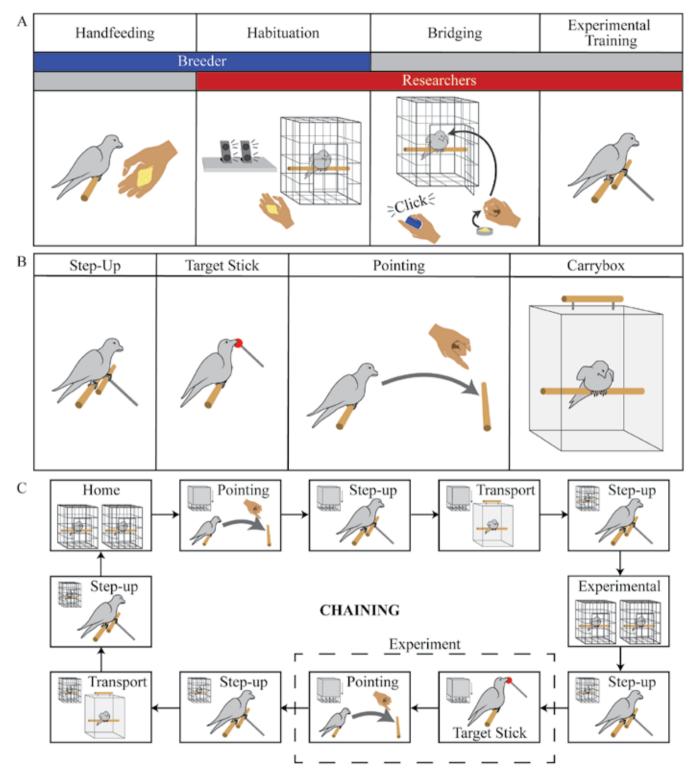
The veterinary team should be involved in all aspects of design, implementation, and review of the program for care of avian species housed in the facility. Because many of these species are not commonly used in research, they are outside of the expertise of many lab animal veterinarians. Specialized training should therefore be sought, or relationships should be developed with specialist avian veterinarians who can aid in the



**Figure 2.** Low-cost custom night-vision system for veterinary and research procedures in the dark, which calms birds and stops them from associating the procedure with the handler. Birds can be habituated to this procedure, to reduce stress further. The system consists of a firstperson view goggle for flying drones, to which an action camera (for example, GoPro) is connected directly through existing communication ports and cables. To enable the camera to see infrared light, the infrared filter is custom-removed by an infrared camera company. To flood the room with infrared light, commercial infrared power LED devices are used. The complete system costs between USD\$500 and USD\$800.

design of routine veterinary care programs and assist with particularly challenging cases. Bird suppliers should be evaluated for quality and health of the birds as part of the quality-assurance program. Frequency of routine exams should be determined according to the duration that birds are housed but, at a minimum, birds should receive visual and physical exams on an annual basis. In addition, routine diagnostics can be performed to screen for any underlying pathologies, and infectious disease testing can be performed to monitor the SPF status of the colony, especially for important zoonotic avian-specific diseases, such as psittacosis. An exhaustive list of avian diseases is beyond the scope of this review, and many useful and well-written textbooks have recently been published.<sup>66,70</sup>

Effective quarantine is essential due to the lack of SPF commercial laboratory bird vendors. Quarantine is important both to protect the colony from the introduction of infectious agents and to protect personnel from potentially zoonotic disease. Due to the stress of capture, transport, and introduction to a new facility, the risk of shedding of many avian and zoonotic disease agents may be significantly higher during this period,<sup>55</sup> increasing the risk of transmission and the importance of an effective quarantine. One positive consequence of this increased shedding is that it may increase the sensitivity of screening tests. Testing should include fecal swabs for Salmonella spp. and Escherichia coli and choanal, conjunctival, and cloacal swabs for Chlamydiaceae. In addition, screening for species-specific disease that may affect individual and colony health is strongly recommended. In wild-caught birds, parasitism can be extensive, so prophylactic treatment can be advantageous. During quarantine, staff entering the facility should wear respiratory protection, such as N95 respirator masks or powered air purifying respirators. Respiratory protection and fit testing should be managed by the institution's occupational health and safety team. Quarantine areas should be housed away from the main colony unless an 'all in, all out' practice is used. In addition,



**Figure 3.** Sample workflow for avian research positive reinforcement training. (A) Timeline of major training steps toward experimental readiness according to the party responsible for task completion. Breeders are responsible for handfeeding of the baby birds until they can eat on their own and for regular handfeeding until shipment of the bird to the research facility, to habituate the bird to human presence. Once at the research husbandry facility, researchers continue handfeeding and play common noises to the birds to continue habituation. Any time a new stimulus is introduced to the birds, a habituation period is necessary. Bridging can overlap with the habituation period and involves a reduction in reward size to a single seed, presented directly after the bridge (often a clicker is used). Once the bridge has been established, training of desired experimental behavior can begin, for example the step-up behavior illustrated. (B) Important behaviors taught during experiment-specific training that allow for ease of transport and voluntary flight performance. Step-up: bird steps onto a perch placed in front of and slightly above the perch on which it is stand. The bird remains on the perch until brought to a new perch, where they voluntarily step-off. Target stick: bird travels to and touches beak to target at end of target stick. The icon demonstrates an approximation toward the full behavior, because a bird often has to fly to get to target stick location. Target stick can be used as a substitute for pointing when more accurate positioning is necessary or for animals that do not respond to pointing. Pointing: bird flies to a perch that researcher points at. Carrybox: bird either flies into a transport box or is brought into one by using a step-up perch. A carrybox is used to transport birds between rooms and buildings. A carrybox is transparent and has 2 large

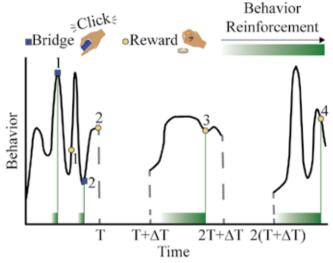


Figure 4. Reward strategy affects precision of behavior reinforcement. This graph displays an example reward schedule for behavior reinforcement, where increase in the y axis represents the behavior to reward. Time T represents a single training session and should be limited to no longer than 2 min. Time  $\Delta T$  represents breaks between training sessions. Bridging reinforces a small timeframe of the behavior, allowing for precise behavior reinforcement, without delays from procuring reward (as indicated by bridge-reward pair 1). However, this precise and narrow window of reinforcement means that slight mistiming of the bridge could reinforce incorrect behavior (bridge-reward pair 2). Lumping refers to rewarding the animal after they have performed a desired behavior; this practice lacks specific indication of what part of the behavior was actually desired; therefore lumping rewards a longer period of behavior, thus potentially reinforcing undesired behavior in addition to desired behavior, as indicated by reward 4. However, lumping can be useful for rewarding longer periods of generally good behavior where there is no specific peak in behavior, such as reward 3.

airflow in the room should be maintained negative to the corridor, to reduce potential environmental contamination of the facility, and recirculation of air should be avoided. Ideally, dedicated staffing and equipment should be used for the quarantine housing. However, if dedicated staffing and equipment cannot be provided, all staff should be made aware that quarantine areas are to be entered last, and staff should change personal protective equipment or work clothes prior to entering the main colony.

A particularly important focus of veterinary care for birds used in flight research is ensuring that their feathers are in optimal condition. Loss of feathers, especially along the wing, often precludes the ability to fly optimally and may result in exclusion of data from the study, although studying bird flight during molt has been informative.<sup>36</sup> The causes of feather loss include ectoparasitism, infectious causes, nutritional disorders, and behavioral disorders. Ectoparasitism can be diagnosed and managed with appropriate medication, and nutritional disorders should be prevented through careful choice of food according to a thorough understanding of the natural biology of the species. Infectious causes include spontaneous local diseases, such as bacterial or fungal infection of the feather follicle, or systemic viral infection such as psittacine beak and feather disease. Pterotillomania (feather plucking) is associated with poor psychologic wellbeing<sup>82</sup> and is often the most challenging underlying cause of feather loss. Feather plucking can be a particular problem in some psittacines because of their long lives, extensive social living, high intelligence, and propensity to develop harmful stereotypic behaviors in barren environments.<sup>34,45</sup> As previously discussed, for these species, having a complex social<sup>49</sup> and physical environment<sup>50,52</sup> which they can interact with, will go some way to mitigate abnormal behavior. Even with a seemingly comprehensive enrichment program, abnormal behavior can develop. Propensity to develop these abnormal behaviors has been associated with anxiety-type character traits<sup>15</sup> as well as genetic and environmental factors.<sup>23</sup> Experienced researchers and animal care staff often recognize anxious birds and try to preempt the development of abnormal behaviors and can even screen them out during the purchasing process. A number of assessment forms are available and can be helpful for recording and monitoring behavior, health, and psychologic wellbeing. This assessment should be performed routinely for all birds kept in research facilities.45

## Alternatives to Avian Models of Flight Research

Flight has evolved independently in several evolutionary lineages due to the strong selection advantages it affords, including energy-efficient habitat exploration and dispersal. This situation has resulted in the evolution of a range of wings that can be studied and whose advantages can be researched and adapted for human use. Alternative models to birds used in flight research include bats,<sup>27</sup> insects,<sup>17</sup> geckos,<sup>32</sup> flying snakes,<sup>31</sup> and even nonanimal models such as seeds.<sup>80</sup> Bats differ from birds in that bats have membranous skin rather than feathers. Given that most man-made flying machines do not use feathers but rather a flat surface, researching the mechanical properties of bat wings may be advantageous.12 Insects provide an invertebrate alternative for flight research, especially for investigating the design and control of miniature drones.<sup>13,43</sup> Insects have been used to understand how flight might be maintained with damaged wings54 or in turbulent environments,59 both of which are important issues that may be encountered by selfflying machines. Although due to their size, insects provide an attractive replacement model for birds, models of flight based from insects can often be limited when scaled up. Therefore, although alternative models of flight do exist, birds are and will remain at the forefront of flight research. Continual evaluation of the care and husbandry of birds used in laboratory research is therefore essential to ensure that their welfare is never compromised and that research goals continue to be achieved.

openings on opposing sides, to train birds to go into the carrybox. The openings ensure that birds do not feel locked in during the first approximations and therefore will go in. The final training step is gradually covering the carrybox for transport. (C) Chaining links individually trained cues to accomplish a set of tasks. The loop shown demonstrates a typical chain used during experimental flight research. Because birds are social animals, at least one other bird is within auditory or visual contact with the experimental bird. However, visual contact is prevented by use of a cage cover when the experimental bird has access to the free space outside of the cages to prevent distraction or undesired flight toward the other bird. The same is true for training in the husbandry space whenever cage doors need to be open during training.

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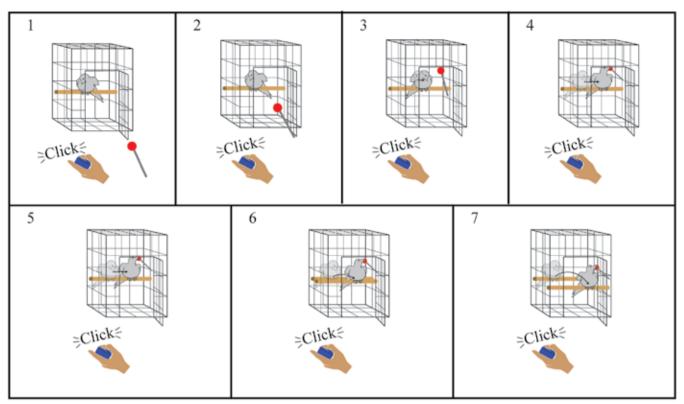


Figure 5. Shaping is a crucial tool for training behaviors, because in general training a behavior requires intermediate steps. The first training step should be a behavior the bird will naturally offer in its repertoire; the subsequent behavioral steps can be built off the initial behavior in a stepwise fashion as the animal naturally varies its behavior until a particular behavior is reinforced, and so on. The steps need to be small enough to ensure a high rate of reinforcement (food rewards) can be maintained to keep the animal engaged. The example shows typical intermediate steps to shape the appropriate behavior for target stick touching, which is an essential husbandry behavior to get animals to move voluntarily to an indicated position. 1: Habituate the bird to the presence of the target stick. Reward the bird for responding correctly to other cues while the trainer holds the target stick within sight of the bird but outside of the cage. 2: The bird is rewarded for not moving away from the target stick when it is placed near the bird. When rewarding, it is key to feed for position, so offer the treat between the bird and the target stick so that the bird voluntary approaches the target stick to get food. Don't force the bird to be close to the target stick by offering the food too close near the target stick. If the bird moves away from the target stick in any way or indicates distress through raised feathers, then withdraw the stimulus to the amount necessary to stop the signs of distress before trying again. As a note, the speed with which the target stick can be presented should increase incrementally also, although an increase in speed and a decrease in distance should not be paired in the same training session (that is, only ask for one additional step in the behavior at a time). 3: Reward the bird for looking toward the target stick when it is placed within the cage. 4: Reward the bird for moving toward the target stick. 5: Reward the bird for moving toward and then touching the target stick with its beak. 6: Reward the bird for stepping from one perch to another nearby perch to touch the target stick. 7: Reward the bird for flying from one perch to another to touch the target stick. Then increase the distance between perches; in other steps, increase the height (angle) between the 2 perches. Only move to the next training step when the success ratio equals or exceeds 80% at or beyond 5 trials; if needed, take a step back. The criterion should be 80% success only, to ensure fluent transitions between each training approximation toward the goal behavior.

#### References

- 1. Animal Welfare Act as Amended. 2008. 7 USC §2131–2156. USA.
- 2. Animal Welfare Regulations. 2008. 9 CFR § 3129.
- 3. Andrada E, Rode C, Blickhan R. 2013. Grounded running in quails: simulations indicate benefits of observed fixed aperture angle between legs before touch-down. J Theor Biol 335:97–107. https://doi.org/10.1016/j.jtbi.2013.06.031.
- Asher L, Bateson M. 2008. Use and husbandry of captive European starlings (*Sturnus vulgaris*) in scientific research: a review of current practice. Lab Anim 42:111–126. https://doi.org/10.1258/la.2007.007006.
- Asher L, Davies GTO, Bertenshaw CE, Cox MAA, Bateson M. 2009. The effects of cage volume and cage shape on the condition and behaviour of captive European starlings (*Sturnus vulgaris*). Appl Anim Behav Sci 116:286–294. https://doi.org/10.1016/j. applanim.2008.10.008.
- Auersperg AMI, von Bayern AMP, Gajdon GK, Huber L, Kacelnik A. 2011. Flexibility in problem solving and tool use of kea and New Caledonian crows in a multi access box paradigm. PLoS One 6:1–8.

- Baier DB, Gatesy SM, Dial KP. 2013. Three-dimensional, highresolution skeletal kinematics of the avian wing and shoulder during ascending flapping flight and uphill flap-running. PLoS One 8:1–16.
- Bateson M. 2010. The use of passerine bird species in laboratory research: implications of basic biology for husbandry and welfare. ILAR J 51:394–408. https://doi.org/10.1093/ilar.51.4.394.
- 9. Biewener A, Dial K, Goslow G. 1992. Pectoralis muscle force and power output during flight in the starling. J Exp Biol 164:1–18.
- Carruthers AC, Thomas AL, Taylor GK. 2007. Automatic aeroelastic devices in the wings of a steppe eagle *Aquila nipalensis*. J Exp Biol 210:4136–4149. https://doi.org/10.1242/jeb.011197.
- Carter J, Lyons NJ, Cole HL, Goldsmith AR. 2008. Subtle cues of predation risk: starlings respond to a predator's direction of eye-gaze. Proc Biol Sci 275:1709–1715. https://doi.org/10.1098/ rspb.2008.0095.
- Cheney JA, Konow N, Middleton KM, Breuer KS, Roberts TJ, Giblin EL, Swartz SM. 2014. Membrane muscle function in the compliant wings of bats. Bioinspir Biomim 9:025007. https://doi. org/10.1088/1748-3182/9/2/025007.

- Chin DD, Lentink D. 2016. Flapping wing aerodynamics: from insects to vertebrates. J Exp Biol 219:920–932. https://doi. org/10.1242/jeb.042317.
- 14. **Chin DD, Lentink D.** 2017. How birds direct impulse to minimize the energetic cost of foraging flight. Sci Adv **3**:1–14.
- Cussen VA, Mench JA. 2015. The relationship between personality dimensions and resiliency to environmental stress in orangewinged Amazon parrots (*Amazona amazonica*), as indicated by the development of abnormal behaviors. PLoS One 10:1–11. https:// doi.org/10.1371/journal.pone.0126170.
- Daugette KF, Hoppes S, Tizard I, Brightsmith D. 2012. Positive reinforcement training facilitates the voluntary participation of laboratory macaws with veterinary procedures. J Avian Med Surg 26:248–254. https://doi.org/10.1647/2011-056.
- 17. Dickinson MH, Lehmann FO, Sane SP. 1999. Wing rotation and the aerodynamic basis of insect flight. Science 284:1954–1960. https://doi.org/10.1126/science.284.5422.1954.
- Emery NJ. 2006. Cognitive ornithology: the evolution of avian intelligence. Philos Trans R Soc Lond B Biol Sci 361:23–43. https:// doi.org/10.1098/rstb.2005.1736.
- 19. Engel S, Bowlin MS, Hedenstrom A. 2010. The role of wind-tunnel studies in integrative research on migration biology. Integr Comp Biol 50:323–335. https://doi.org/10.1093/icb/icq063.
- 20. Fair J, Paul E, Jones J. 2010. Guidelines to the use of wild birds in research, 3rd ed. Washington (DC): Ornithological Council.
- 21. **Federation of Animal Science Societies.** 2010. Guide for the care and use of agricultural animals in research and teaching, 3rd ed. Champaign (IL): Federation of Animal Science Societies.
- Garner JP, Mason GJ, Smith R. 2003. Stereotypic route-tracing in experimentally caged songbirds correlates with general behavioural disinhibition. Anim Behav 66:711–727. https://doi. org/10.1006/anbe.2002.2254.
- Garner JP, Meehan CL, Famula TR, Mench JA. 2006. Genetic, environmental, and neighbor effects on the severity of stereotypies and feather picking in Orange-winged Amazon parrots (*Amazona amazonica*): An epidemiological study. Appl Anim Behav Sci 96:153–168. https://doi.org/10.1016/j.applanim.2005.09.009.
- Greer WG, Banks RE. 2016. The IACUC administrator's guide to animal program management. Boca Raton (FL): CRC Press. https://doi.org/10.1201/b19188
- Hawkins P, Morton DB, Cameron D, Cuthill I, Francis R, Freire R, Gosler A, Healy S, Hudson A, Inglis I, Jones A, Kirkwood J, Lawton M, Monaghan P, Sherwin C, Townsend P. Members of the Joint Working Group on Refinement. 2016. Laboratory birds: refinements in husbandry and procedures. Fifth report of BVAAWF/ FRAME/RSPCA/UFAW Joint Working Group on Refinement. Lab Anim 35 Suppl 1:1–163. https://doi.org/10.1258/0023677011911967.
- 26. Health Research Extension Act. 1985. Public Law 99-158. Washington (DC): Government Printing Office.
- Hedenström A, Johansson LC. 2015. Bat flight: aerodynamics, kinematics and flight morphology. J Exp Biol 218:653–663. https:// doi.org/10.1242/jeb.031203.
- Hedrick TL, Tobalske BW, Biewener AA. 2003. How cockatiels (*Nymphicus hollandicus*) modulate pectoralis power output across flight speeds. J Exp Biol 206:1363–1378. https://doi.org/10.1242/ jeb.00272.
- 29. Institute for Laboratory Animal Research. 2011. Guide for the care and use of laboratory animals, 8th ed. Washington (DC): National Academies Press.
- 30. Jackson BE, Dial KP. 2011. Scaling of mechanical power output during burst escape flight in the Corvidae. J Exp Biol **214**:452–461. https://doi.org/10.1242/jeb.046789.
- 31. Jafari F, Ross SD, Vlachos PP, Socha JJ. 2014. A theoretical analysis of pitch stability during gliding in flying snakes. Bioinspir Biomim 9:025014. https://doi.org/10.1088/1748-3182/9/2/025014.
- 32. Jusufi A, Kawano DT, Libby T, Full RJ. 2010. Righting and turning in mid-air using appendage inertia: reptile tails, analytical models and bio-inspired robots. Bioinspir Biomim 5:045001. https://doi.org/10.1088/1748-3182/5/4/045001.
- Kalmar ID. 2010. Guidelines and ethical considerations for housing and management of psittacine birds used in research. <u>ILAR J</u> 51:409–423. https://doi.org/10.1093/ilar.51.4.409.

- Kalmar ID, Moons CP, Meers LL, Janssens GP. 2007. Psittacine birds as laboratory animals: refinements and assessment of welfare. J Am Assoc Lab Anim Sci 46:8–15.
- Kim LC, Garner JP, Millam JR. 2009. Preferences of Orangewinged Amazon parrots (*Amazona amazonica*) for cage enrichment devices. Appl Anim Behav Sci 120:216–223. https://doi. org/10.1016/j.applanim.2009.06.006.
- KleinHeerenbrink M, Hedenström A. 2016. Wake analysis of drag components in gliding flight of a jackdaw (*Corvus monedula*) during moult. Interface Focus 7:1–13. https://doi.org/10.1098/ rsfs.2016.0081.
- 37. Kress D, van Bokhorst E, Lentink D. 2015. How lovebirds maneuver rapidly using super-fast head saccades and image feature stabilization. PLoS One 10:1–24.
- Kruyt JW, Quicazán-Rubio EM, van Heijst GF, Altshuler DL, Lentink D. 2014. Hummingbird wing efficacy depends on aspect ratio and compares with helicopter rotors. J R Soc Interface 11:1–12.
- Lentink D. 2014. Bioinspired flight control. Bioinspir Biomim 9:1–8. https://doi.org/10.1088/1748-3182/9/2/020301.
- Lentink D. 2016. Coevolving advances in animal flight and aerial robotics. Interface Focus 7:1–6. https://doi.org/10.1098/ rsfs.2016.0119.
- 41. Lentink D, Biewener AA. 2010. Nature-inspired flight-beyond the leap. Bioinspir Biomim 5:1–9. https://doi.org/10.1088/1748-3182/5/4/040201.
- Lentink D, Haselsteiner AF, Ingersoll R. 2015. In vivo recording of aerodynamic force with an aerodynamic force platform: from drones to birds. J R Soc Interface 12:1–5. https://doi.org/10.1098/ rsif.2014.1283.
- 43. Liu H, Ravi S, Kolomenskiy D, Tanaka H. 2016. Biomechanics and biomimetics in insect-inspired flight systems. Philos Trans R Soc Lond B Biol Sci **371:**1–11.
- Lockwood R, Swaddle JP, Rayner JMV. 1998. Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. J Avian Biol 29:273–292. DOI: 10.2307/ 3677110
- Luescher AU, Wilson L. 2006. Housing and management considerations for problem prevention, p 291–299. In: Luescher AU, editor. Manual of parrot behavior. Oxford (United Kingdom): Blackwell Publishing.
- Mahjoub G, Hinders MK, Swaddle JP. 2015. Using a "sonic net" to deter pest bird species: Excluding European starlings from food sources by disrupting their acoustic communication. Wildl Soc Bull 39:326–333. https://doi.org/10.1002/wsb.529.
- Mattison S. 2012. Training birds and small mammals for medical behaviors. Vet Clin North Am Exot Anim Pract 15:487–499. https:// doi.org/10.1016/j.cvex.2012.06.012.
- 48. McGreevy P, Boakes R. 2007. Carrots and sticks: principles of animal training. Cambridge (United Kingdom): Cambridge University Press.
- 49. Meehan CL, Garner JP, Mench JA. 2003. Isosexual pair housing improves the welfare of young Amazon parrots. Appl Anim Behav Sci 81:73–88. https://doi.org/10.1016/S0168-1591(02)00238-1.
- 50. Meehan CL, Garner JP, Mench JA. 2004. Environmental enrichment and development of cage stereotypy in Orange-winged Amazon parrots (*Amazona amazonica*). Dev Psychobiol 44:209–218. https://doi.org/10.1002/dev.20007.
- Meehan CL, Mench JA. 2002. Environmental enrichment affects the fear and exploratory responses to novelty of young Amazon parrots. Appl Anim Behav Sci 79:75–88. https://doi.org/10.1016/ S0168-1591(02)00118-1.
- 52. Meehan CL, Millam JR, Mench JA. 2003. Foraging opportunity and increased physical complexity both prevent and reduce psychogenic feather picking by young Amazon parrots. Appl Anim Behav Sci 80:71–85. https://doi.org/10.1016/S0168-1591(02)00192-2.
- 53. Mills AD, Crawford LL, Domjan M, Faure JM. 1997. The behavior of the Japanese or domestic quail *Coturnix japonica*. Neurosci Biobehav Rev 21:261–281. https://doi.org/10.1016/ S0149-7634(96)00028-0.

- Muijres FT, Iwasaki NA, Elzinga MJ, Melis JM, Dickinson MH. 2017. Flies compensate for unilateral wing damage through modular adjustments of wing and body kinematics. Interface Focus 7:1–12.
- 55. Nakamura M, Nagamine N, Takahashi T, Suzuki S, Kijima M, Tamura Y, Sato S. 1994. Horizontal transmission of Salmonella enteritidis and effect of stress on shedding in laying hens. <u>Avian</u> Dis 38:282–288. https://doi.org/10.2307/1591950.
- Nicol CJ, Pope SJ. 1999. The effects of demonstrator social status and prior foraging success on social learning in laying hens. Anim Behav 57:163–171. https://doi.org/10.1006/anbe.1998.0920.
- 57. Office of Laboratory Animal Welfare. 2015. Public health service policy on humane care and use of laboratory animals. Bethesda (MD): National Institutes of Health.
- Office of Laboratory Animal Welfare. [Internet]. 2018. Frequently asked questions - PHS Policy on humane care and use of laboratory animals. [Cited 18 January 2018]. Available at: https://grants.nih. gov/grants/olaw/faqs.htm.
- Ortega-Jimenez VM, Mittal R, Hedrick TL. 2014. Hawkmoth flight performance in tornado-like whirlwind vortices. Bioinspir Biomim 9:025003. https://doi.org/10.1088/1748-3182/9/2/025003.
- Peron F, Rat-Fischer L, Lalot M, Nagle L, Bovet D. 2011. Cooperative problem solving in African grey parrots (*Psittacus erithacus*). Anim Cogn 14:545–553. https://doi.org/10.1007/s10071-011-0389-2.
- 61. **Ramirez K.** 1999. Animal training: successful animal management through positive reinforcement. Chicago (IL): Shedd Aquarium.
- 62. **Rattenborg NC.** 2017. Sleeping on the wing. Interface Focus 7:1–14.
- Reynolds KV, Thomas AL, Taylor GK. 2014. Wing tucks are a response to atmospheric turbulence in the soaring flight of the steppe eagle *Aquila nipalensis*. J R Soc Interface 11:1–11. https:// doi.org/10.1098/rsif.2014.0645.
- 64. Roberts TJ, Marsh RL, Weyand PG, Taylor CR. 1997. Muscular force in running turkeys: the economy of minimizing work. Science 275:1113–1115. https://doi.org/10.1126/science.275.5303.1113.
- Sachs G. 2015. New model of flap-gliding flight. J Theor Biol 377:110–116. https://doi.org/10.1016/j.jtbi.2015.03.022.
- 66. Samour J. 2016. Avian medicine, 3rd ed. St. Louis (MO): Elsevier.
- Schmidt MF. 2010. An IACUC perspective on songbirds and their use in neurobiological research. ILAR J 51:424–430. https://doi. org/10.1093/ilar.51.4.424.
- Seibert LM. 2006. Social behavior of psittacine birds, p 255–265. In: Luescher AU, editor. Manual of parrot behavior. Oxford (United Kingdom): Blackwell Publishing.
- Silverman J, Suckow MA, Sreekant M, editors. 2014. The IACUC handbook, 3rd ed. Boca Raton (FL): CRC Press. https://doi. org/10.1201/b16915

- 70. **Speer BL.** 2016. Current therapy in avian medicine and surgery. 1st ed. St Louis (MO): Elsevier.
- Spivey RJ, Bishop CM. 2013. Interpretation of body-mounted accelerometry in flying animals and estimation of biomechanical power. J R Soc Interface 10:1–15. https://doi.org/10.1098/ rsif.2013.0404.
- 72. **Swaddle JP, Ingrassia NM.** 2017. Using a sound field to reduce the risks of bird-strike: an experimental approach. Integr Comp Biol **57**:81–89. https://doi.org/10.1093/icb/icx026.
- Taylor GK, Bacic M, Bomphrey RJ, Carruthers AC, Gillies J, Walker SM, Thomas AL. 2008. New experimental approaches to the biology of flight control systems. J Exp Biol 211:258–266. https://doi.org/10.1242/jeb.012625.
- 74. Tobalske BW. 2007. Biomechanics of bird flight. J Exp Biol 210:3135–3146. https://doi.org/10.1242/jeb.000273.
- 75. **Tobalske BW.** 2010. Hovering and intermittent flight in birds. Bioinspir Biomim **5:**045004. DOI: 10.1088/1748-3182/5/4/045004
- Tobalske BW. 2015. Morphology, velocity, and intermittent flight in birds. Integr Comp Biol 41:177–187. https://doi.org/10.1093/ icb/41.2.177.
- Tobalske BW, Peacock WL, Dial KP. 1999. Kinematics of flapbounding flight in the zebra finch over a wide range of speeds. J Exp Biol 202:1725–1739.
- Tobalske BW, Puccinelli LA, Sheridan DC. 2005. Contractile activity of the pectoralis in the zebra finch according to mode and velocity of flap-bounding flight. J Exp Biol 208:2895–2901. https:// doi.org/10.1242/jeb.01734.
- 79. Tucker VA. 1995. Drag reduction by wing tip slots in a gliding Harris' hawk, *Parabuteo unicinctus*. J Exp Biol **198:**775–781.
- Ulrich ER, Pines DJ, Humbert JS. 2010. From falling to flying: the path to powered flight of a robotic samara nano air vehicle. Bioinspir Biomim 5:045009. https://doi.org/10.1088/1748-3182/5/4/045009.
- van Leeuwen JL, Sokoloff AJ, Goslow GE. 1999. Neuromuscular organization of avian flight muscle: architecture of single muscle fibres in muscle units of the pectoralis (*pars thoracicus*) of pigeon (*Columba livia*). Philos Trans R Soc Lond B Biol Sci 354:917–925. https://doi.org/10.1098/rstb.1999.0443.
- van Zeeland YRA, Spruit BM, Rodenburg TB, Riedstra B, van Hierden YM, Buitenhuis B, Korte SM, Lumeij JT. 2009. Feather damaging behaviour in parrots: A review with consideration of comparative aspects. Appl Anim Behav Sci 121:75–95. https:// doi.org/10.1016/j.applanim.2009.09.006.
- Warrick DR, Tobalske BW, Powers DR. 2005. Aerodynamics of the hovering hummingbird. Nature 435:1094–1097. https://doi. org/10.1038/nature03647.