The Use of Passerine Bird Species in Laboratory Research: Implications of Basic Biology for Husbandry and Welfare

Melissa Bateson and Gesa Feenders

Abstract

Passerine birds are important models in fundamental biological research, with as many as 300,000 individuals used in laboratory experiments worldwide annually. However, because the use of passerines is rare compared with that of more conventional laboratory animals, there is often a lack of information about the basic biology and husbandry requirements of these species. We aim to address this deficit by providing an overview of the most salient aspects of passerine biology and their implications for laboratory husbandry and welfare. We start by describing the characteristics that make these birds useful and interesting research subjects. Specifically, we highlight features (e.g., birdsong) of passerine biology that differentiate these birds from more common laboratory animals. Next, we consider the implications of passerine biology for husbandry in the laboratory. Many of the aspects of passerine biology that make these species valuable to scientists are also likely to be affected by environmental variables; a good knowledge of these variables is necessary in order to choose appropriate laboratory conditions for passerines. We outline how the developmental history of the birds and choices of caging, feeding, and environmental regimes might influence their physiology and behavior and thus affect both the welfare of the birds and the quality of the resulting data. We stress the importance of a sound understanding of the biology of any species to ensure good welfare and good science.

Key Words: animal numbers; avian husbandry; bird; passerine; songbird; welfare

Introduction: Passerine Birds and Their Use in Research

The Passeriformes, more commonly known as the passerines, are a large order of perching birds found in most terrestrial habitats. They include many common garden birds such as tits and chickadees, sparrows, thrushes, starlings, members of the crow family, and domesticated aviary species such as the zebra finch and canary. There are 5712 species of passerines, which is over half the known species of birds (Sibley and Monroe 1990).

The passerine lineage is as old as that of mammals, having diverged from the rest of the birds around 80 million years ago, and is morphologically, ecologically, and behaviorally diverse. Passerines range in size from the smallest pygmy tyrants (*Myiornis atricapillus*) at about 4.2 g up to the thick-billed ravens (*Corvus crassirostris*) at 1500 g; they occupy most ecological niches (although none are truly aquatic), with some species such as the European starling (*Sturnus vulgaris*) now found on all continents other than Antarctica (Feare 1984); and they vary in range size, foraging behavior, degree of sociality, reproductive behavior, and complexity of vocalizations.

Passerine species are widely used in laboratory-based research; to quantify this use, we conducted a systematic review of recent research on passerine birds (see Box 1 for methods). Focusing on papers published in 2008, we identified 271 primary empirical studies using captive passerine species worldwide; most took place in laboratories in the United States, and European countries were the next highest source (Figure 1). We estimated that the research described in these papers likely represents the use of approximately 151,000 to 215,000 birds annually (see Box 2 for methods), but this could be a substantial underestimate because the national statistics that we used to compute these estimates include only birds used in invasive procedures. Because about a third of the papers we reviewed did not involve invasive procedures, it is possible that the annual estimates of bird use may be as much as 226,500 to 322,500.

Of the nearly 40 different passerine species used in laboratory research identified in our review, we found that the three most commonly used were the zebra finch (*Taeniopygia guttata*), the European starling (*Sturnus vulgaris*), and the house sparrow (*Passer domesticus*); corvids, parids, various finches, and American sparrows account for many of the others (Table 1). Interestingly, only half of the studies used domesticated species that readily breed in captivity (i.e., zebra finches, Bengalese finches, and canaries); commonly used species such as the European starling are always taken from the wild either as adults or as chicks for hand raising (Asher and Bateson 2008). This is significant because the revised version of

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Melissa Bateson, MA, DPhil, is Reader in Ethology and Gesa Feenders, PhD, is a research associate at the Centre for Behaviour and Evolution and the Institute of Neuroscience at Newcastle University.

Address correspondence and reprint requests to: Dr. Melissa Bateson, Institute of Neuroscience, Henry Wellcome Building for Neuroecology, Framlington Place, Newcastle upon Tyne NE2 4HH, United Kingdom or email melissa.bateson@ncl.ac.uk.

Box 1 Literature review of passerine use: methodology

To obtain an estimate of recent passerine use in laboratory research, we reviewed scientific papers listed on Web of Science (www.ISIWebofKnowledge.com) for the year 2008. We restricted our search to studies that described primary empirical research on passerine birds and involved keeping the birds in captivity for a minimum of 24 hours. We included all studies that met these criteria, independent of whether the research involved procedures thought to involve pain, suffering, distress, or lasting harm. We did not include field-based studies because we wanted our review to reflect laboratory use of passerines.

Because "passerine" is rarely listed in titles, abstracts, or key words, we searched for papers listing individual species names. It was not feasible to perform searches for every passerine species, so we compiled a list of species that we know are used in laboratory research based on our own expertise and consultation with colleagues. The resulting list of species is therefore unlikely to be comprehensive, but we are confident that it includes the most commonly used species in the time period we considered.

Generally, using the Latin name as the search term was sufficient to identify all the relevant papers on that species. However, in the case of some particularly widely used domesticated species, the Latin name alone proved inadequate. For example, the search for "*Taeniopygia guttata*" returned 116 papers 65 of which contained primary empirical studies of zebra finches, and that for papers containing "zebra finch*" but not "*Taeniopygia guttata*" returned an additional 152 papers, 41 of which described laboratory studies. Therefore, for the zebra finch, Bengalese finch, and canary we performed searches using both the Latin and common names so as not to miss relevant papers.

For all papers identified, where the full text was available to us, we scanned the methods section for the number of birds used and the country in which the research was performed. Table 1 presents the number of papers per species, the number of papers for which we could determine the number of birds used (n), the mean number of birds used per study, and the total number of birds used in the studies for which we obtained n. We also determined whether the research involved any procedures involving pain, suffering, distress, or lasting harm that would imply that the work required licensing by the Home Office if it were conducted in the United Kingdom.

European Union Directive 86/609 (www.ecbr.eu/directive-86609_2.htm) on the protection of animals used in research seeks to ban the use of animals taken from the wild.

Our review suggests that most research on passerines falls under the category of fundamental biological research. The most common reason for studying passerines is their song, but, as we note below, there are a number of other reasons that researchers choose these species. In addition to fundamental science, there is also (more limited) use in applied research areas such as agricultural pest control, ecotoxicology, and epidemiology of infectious disease (e.g., Gill and Paperna 2008; Hile 2004; Talloen et al. 2008).

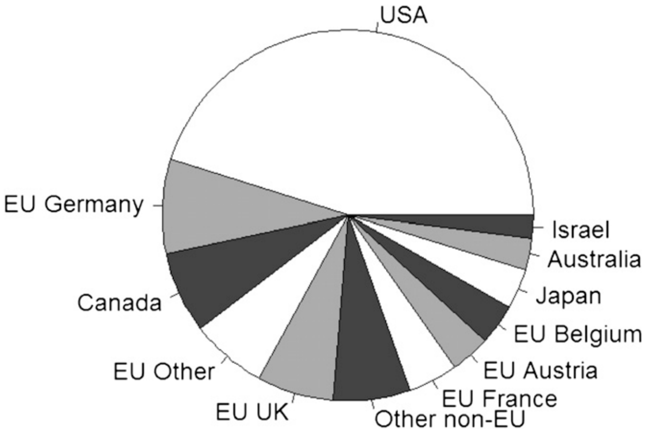

Figure 1 Pie chart showing the percentage of studies on passerine birds performed in different countries based on our review of the literature published in 2008. These figures are based on the subset of 255 papers (94.1%) for which the country in which the work was performed could be inferred; papers were omitted if the authors' addresses included more than one country and there was no statement of where the research was conducted. European Union (EU) countries with >3% of the papers are individually identified; "EU other" includes Bulgaria, Estonia, Finland, Italy, Netherlands, Romania, Spain, and Sweden; "other non-EU" includes Argentina, Brazil, China, Mexico, Norway, Russia, Saudi Arabia, South Africa, and Switzerland.

The numbers presented above highlight the importance of passerine species in research around the world. However, because their use is rare compared with that of more conventional laboratory animals (passerines accounted for less than 0.37% of the animals used in licensed procedures in the United Kingdom in 2005), these species have been largely neglected in research on laboratory animal husbandry and welfare. As a result, animal facility inspectors, managers, and technicians are often poorly informed about the basic biology and husbandry requirements of these birds. It is also possible that some scientists whose training does not include whole-organism biology are unaware of aspects of passerine biology that might have important implications for their research.

In this article we aim to address the above deficits by providing a broad overview of the most salient aspects of passerine biology and their implications for the husbandry and welfare of these species in the laboratory. We start by describing the characteristics that make these birds useful and interesting research subjects; specifically, we highlight features of their biology that differentiate these species from more common laboratory animals. We then examine the implications of the biology of passerines for their husbandry in the laboratory. Many of the aspects of passerine biology

Box 2 How many passerines are used in laboratory research annually?

Estimating the total numbers of passerine birds used in laboratory research worldwide is difficult because no country reports its animal use statistics at this level of taxonomic detail. The United Kingdom probably comes closest, as the Home Office (HO) statistics on animals used in licensed procedures (i.e., procedures considered to have the potential to cause "pain, suffering, distress, or lasting harm") divide birds into five categories: domestic fowl (*Gallus domesticus*), turkey, quail (*Coturnix coturnix*), quail (not *Coturnix coturnix*), and "other bird" (Home Office 2009). The HO's "other bird" category is likely to be predominantly passerines, with the addition of some other groups including pigeons, parakeets, game birds, and sea birds. When we asked the HO for exact numbers of passerines used in 2008 we received the following statement: "Passerines of a wide range of species are thought to account for a significant proportion of the 9,120 'other birds' based on the information received as part of the data collection, however exact numbers are not available" (Meg Hillier, UK Home Office, January 21, 2010). The "other bird" figure is therefore an overestimate of the number of passerines used in licensed procedures in the United Kingdom. However, the HO statistics do not include passerines used in nonlicensed procedures, so there is reason to believe that the figure might underestimate total passerine use. We judged that approximately 33% of the papers that we surveyed in our literature review did not involve procedures that would be licensable in the United Kingdom, suggesting that as much as one third of research on passerines might not be captured in the HO figures. For want of better information, we used the UK HO's "other bird" figure as the best available estimate of a country's annual use of passerine birds. Despite an increase in total animal use, the use of "other birds" reported to the HO has been approximately stable for the period 2000-2008 at a mean of 9475 birds per year (Figure 2).

We used the HO "other bird" figure to estimate worldwide passerine bird use by two different approaches. Our first was to compute the proportion of all animal use in the United Kingdom that is attributable to other birds, and to multiply this number by the best estimate of total worldwide laboratory animal use; the most comprehensive attempt to estimate worldwide laboratory animal use produced a conservative estimate of 58.3 million individuals in 2005 (Taylor et al. 2008). We used the HO figures for the United Kingdom in 2005 to calculate the proportion of animal use attributable to other birds at 0.37%. Multiplying these figures yields an estimate of worldwide "other bird" use in 2005 of 214,642 birds. However, this estimate is based on the assumption that the proportion of scientific research on passerines in the United Kingdom is similar to that in other countries, which is unlikely to be correct. The United Kingdom has a particularly strong tradition of ethological research involving passerines, and as such is more than twice as strongly represented in Figure 1 (6.7%) than would be expected on the basis of its total animal use figures (3.2% of the worldwide total of 58.3 million according to the figures in Taylor et al. 2008). We therefore consider this figure the upper limit of our estimate.

Our second approach was based on the data obtained from our literature review. We used the mean number of birds per study of 39.4 (see Table 1) to estimate the total number of birds used in the 17 papers published in the United Kingdom in 2008 at 670. We then used this number to derive the scaling factor of 14.11 relating bird use derived from the sample sizes reported in scientific papers published in 2008 to "other bird" use according to the HO statistics for 2007 (we used 2007 figures because we assumed a 1-year lag, as in Taylor et al. 2008, between bird use and publication). Total worldwide passerine use in 2007 was then estimated as the number of studies published in 2008 identified in our review (271), multiplied by the average number of birds used per study (39.4), multiplied by the scaling factor (14.11), resulting in 150,658 birds. We consider this the lower limit of our estimate, since we might have missed some papers from our review, and many studies don't get published at all.

We therefore conservatively estimate total annual passerine use for the period 2005-2007 at between 150,658 and 214,642 birds. It should be noted that these two estimates are not independent because they both rely on UK HO figures (which are likely to underestimate total passerine use due to their exclusion of unlicensed procedures).

that make these species valuable to scientists are also likely to be affected by environmental variables that can be controlled in the laboratory. Facility managers and scientists must therefore understand the potential effects of these variables in order to choose appropriate conditions for laboratory passerines. We describe how the birds' developmental history and choices of caging, feeding, and environmental regimes might affect the physiology and behavior of passerines in the laboratory as well as the birds' welfare and the quality of the resulting data. Overall, our aim is to stress the importance of a sound understanding of the biology of these (and indeed any) species to ensure both the welfare of individual animals in the laboratory and the quality of the scientific results.

Why Study Passerines?

There are a number of practical, historical, and biological considerations that make passerine birds useful subjects for fundamental biological research. In contrast to rats and mice, passerines are typically diurnal, making them relatively easy to observe in both the wild and the laboratory. They are also physically attractive because of the diversity of their plumage colors and behavior. For these reasons, passerines have historically been very heavily studied by both amateur and professional ornithologists, with the result that the order has probably the best-documented behavior and ecology of any animal group. This wealth of information makes the passerines invaluable for any type of comparative research aimed

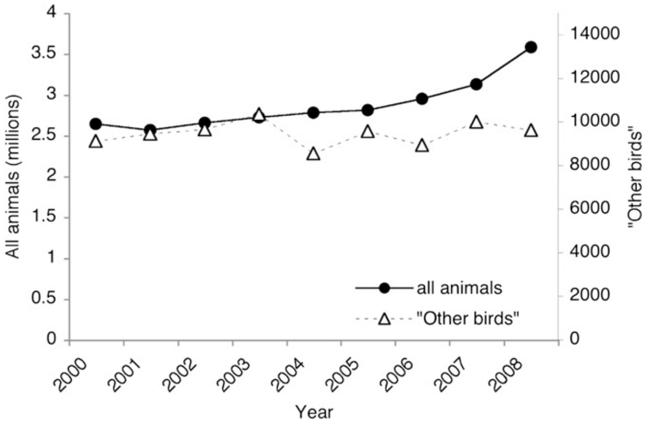

Figure 2 Numbers of all animals and of the subset designated as "other birds" (our best estimate of passerine use; see Box 2 for details) used in research in the United Kingdom since 2000. Numbers are from statistics collected by the UK Home Office relating to scientific procedures performed on living animals under the provisions of the Animals (Scientific Procedures) Act 1996 (full reports are available at www.homeoffice.gov.uk/rds/scientific1.html). Note that although the total number of animals used is increasing, the number of "other birds" used appears to be approximately stable.

at elucidating the adaptive significance and evolution of biological traits. The recent sequencing of the zebra finch genome (Warren et al. 2010) additionally opens up exciting new possibilities for comparative genetic analysis, especially in relation to behavioral and cognitive abilities not well represented in the more standard model species used in genetics (Clayton et al. 2009).

Passerine species are often chosen as research subjects because they exhibit traits that are not found in more standard laboratory animals such as rats, mice, and galliform birds (e.g., chickens, quail, turkeys). These traits are interesting topics for research in their own right, but, as we discuss below, also provide useful models for the study of biological phenomena relevant to scientific understanding of human behavior and cognition. In the following sections we briefly review some of the main aspects of passerine biology that differentiate these birds from other laboratory animals and make them attractive to researchers. We do not aim to provide comprehensive reviews of each topic but rather to give a flavor of the research opportunities available with passerines and to point interested readers to exciting recent findings and more extensive reviews.

Song

All passerines sing, and birdsong is undoubtedly the main behavior pattern that attracts researchers to this group. Passerines have dedicated neural pathways for song learning and production (the "song system") that are the subject of extensive research in behavioral neuroscience (Brainard and Doupe 2002; Prather and Mooney 2004). Since vocal communication is so prominent in birds, there is also considerable research interest in both sensory and cognitive aspects of song perception and discrimination (e.g., Bloomfield et al. 2008; Gentner et al. 2006; Itatani and Klump 2009; van Heijningen et al. 2009). Moreover, because song is a means of communication, it plays a very important social function in mate choice and group organization (White 2010).

Taxonomically passerines are split into two suborders: first, the oscines or songbirds, which are the majority and learn songs via auditory input from other individuals; and second, the less speciose suboscines, which also sing but have a simpler syrinx and are traditionally believed not to acquire their songs via learning (Catchpole and Slater 1995). The evolution of vocal learning is rare (among nonavian groups it occurs only in humans[1] and cetaceans, with some limited evidence of it in bats, seals, and elephants). Although all oscines learn their songs, there is considerable variation between species in both the complexity of song and the type of experience required for a bird to develop normal adult song, topics that have been extensively studied by behavioral biologists (Catchpole and Slater 1995; also see White 2010 in this issue).

The oscine song system arguably represents the best example so far of the neurobiology underlying a complex behavioral trait and has been the source of numerous important discoveries for mammalian neuroscience. The first reports of adult neurogenesis were made in the canary song system (Goldman and Nottebohm 1983); studies of the song system have been influential in understanding the effect of sex hormones on brain dimorphism (Grisham et al. 2008; Schlinger 1998); and mirror neurons, hypothesized to be important in motor learning in primates, have recently also been discovered in songbirds (Prather et al. 2008). The recent development of fMRI for songbirds is an advantageous technical innovation in the study of bird song (Van Meir et al. 2005).

Flight and Navigation

All passerines fly—some species (e.g., warblers, finches, white-eyes, and starlings) migrate over long distances—and thus are suitable subjects for studying the anatomical, physiological, and behavioral adaptations that flight entails (Hedenström 2002). The recent use of wind tunnels to study the physiology of birds in flight is greatly increasing understanding of the biology of flight (e.g., Engel et al. 2006; Johansson and Hedenström 2009; Schmidt-Wellenburg et al. 2008). During migratory season passerines housed in the laboratory exhibit migratory restlessness (*Zugunruhe*; Kramer 1949), which makes them suitable for study of the mechanisms underlying migration.

There has been considerable research interest in the sensory and cognitive mechanisms involved in navigation, including the possible use of magnetoreception (Wiltschko et al.

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[1] The parallels between birdsong learning and human language acquisition have recently led to the use of songbirds as important models for understanding the acquisition and production of language (Jarvis 2004; Doupe and Kuhl 1999; Rosenfield et al. 2000).

Table 1 Survey of passerine bird use in research: Species with at least two laboratory studies listed in the Web of Science for 2008

Species name		Family	Types of research	Statistics for 2008 papers			
Latin	**Common**			**# papers**	**# papers with n**	**birds/study (mean ± SEM)**	**Total birds**
Taeniopygia guttata[a]	Zebra finch	Estrildidae	Behavioral neuroscience, neurobiology of song learning and production, hearing, physiology, welfare	108	71	47.3 ± 6.3	3356
Sturnus vulgaris and *S. roseus*	Starling (European and rose-colored)	Sturnidae	Behavior, behavioral ecology, cognition, song, ecotoxicology, endocrinology (molt, reproduction, stress), physiology of flight, welfare	26	22	27.5 ± 5.9	606
Passer domesticus	House sparrow	Passeridae	Ecotoxicology, immunology, parasitology, physiology	21	17	42.1 ± 8.6	715
Lonchura striata[a]	Bengalese finch	Estrildidae	Song learning	15	6	16.7 ± 4.2	100
Corvus corax, C. frugilegus, C. monedula, and *C. moneduloides*	Raven, rook, jackdaw, and New Caledonian crow	Corvidae	Behavior, cognition (memory, future planning, tool use and manufacture, social cognition), neurobiology	15	14	11.5 ± 1.3	161
Serinus canaria[a]	Canary	Fringillidae	Song, veterinary medicine	14	13	51.5 ± 11.1	669
Parus major	Great tit	Paridae	Physiology, behavior (personality), coloration	12	7	67.4 ± 31.6	472
Zonotrichia leucophrys and *Z. ablicollis*	White-crowned and white-throated sparrows	Emberizidae	Song	11	10	28.6 ± 5.0	286
Carpodacus mexicanus	House finch	Fringillidae	Behavior, parasitology	7	5	64.4 ± 16.5	322
Poecile atricapillus and *P. gambeli*	Chickadee (black-capped and mountain)	Paridae	Behavior, cognition	5	5	28.6 ± 4.9	143
Molothrus ater	Brown-headed cowbird	Icteridae	Behavioral ecology, social behavior	4	2	62.5 ± 9.2	125
Melospizia melodia	Song sparrow	Emberizidae	Song	3	1	31.0	31
Cyanistes caeruleus	Blue tit	Paridae	Behavior, development	3	2	91.0 ± 26.9	182

Table 1 (Continued)

Species name		Family	Types of research	Statistics for 2008 papers			
Latin	**Common**			**# papers**	**# papers with n**	**birds/study (mean ± SEM)**	**Total birds**
Aimophila carpalis, A. cassinii, and *A. ruficeps*	Rufous-winged, Cassin's, and rufous-crowned sparrows	Emberizidae	Physiology, behavior	3	3	32.3 ± 2.5	97
Nucifraga columbiana	Clark's nutcracker	Corvidae	Behavior, cognition (memory)	3	2	4.5 ± 0.7	9
Cinnyris talatala	White-bellied sunbird	Nectariniidae	Behavior	3	2	7.5 ± 0.7	15
Cardinalis cardinalis	Northern cardinal	Cardinalidae	Song	2	1	20.0	20
Junco hyemalis	Dark-eyed junco	Emberizidae	Morphology, physiology, and behavior	2	2	48.5 ± 30.4	97
Sylvia borin	Garden warbler	Sylviidae	Behavior, cognition, migration	2	2	53.5 ± 48.8	107
Erithacus rubecula	European robin	Muscicapidae	Behavior, cognition, migration	2	2	28.0 ± 17.0	56
Carduelis chloris	Greenfinch	Fringillidae	Development of plumage coloration	2	2	57.0 ± 52.3	114
Other species with a single study[b]				8	6	14.3 ± 8.3	86
Totals				271	197	39.4 ± 3.0	7769

[a] Domesticated species

[b] These species were *Acrocephalus arundinaceus* (great reed warbler), *Aphelocoma californica* (western scrub jay), *Gymnorhinus cyanocephalus* (pinyon jay), *Phyliodonyris novaehollandiae* (Australian New Holland honeyeater), *Pica pica* (magpie), *Pitangus sulfuratus* (great kiskadee), *Sitta Canadensis* (red-breasted nuthatch), and *Zosterops lateralis* (Australian white eye).

2010; Zapka et al. 2009) and sensitivity to polarized light (Muheim et al. 2007).

Mate Choice and Sexual Selection

Birds provide some of the best examples of intersexual selection, since many species exhibit sexual dimorphism of appearance and behavior. Sexually dimorphic passerines such as the zebra finch have been widely used to study female choice for complex sexually selected traits such as plumage, song, and other behavioral displays (Bro-Jorgensen et al. 2007; Byers and Kroodsma 2009; Griggio et al. 2007). Recent studies have explored the connections between nutrition, body condition, and plumage coloration in the context of sexual attractiveness (e.g., Peters et al. 2008). The importance of color in avian intraspecific signaling has prompted research interest in color vision in passerine birds, and specifically use of the ultraviolet (UV) part of the spectrum in mate choice (Bennett et al. 1996, 1997).

Foraging

Birds are good subjects for fundamental studies of foraging behavior because they have high metabolic rates resulting in high food requirements. Passerines (specifically European starlings, corvids, and parids) can be trained to obtain food in the laboratory through a variety of operant techniques such as pecking a key (Stephens and Anderson 2001), touching a computer screen (Biegler et al. 2001), digging in sand (Bean et al. 1999), or flying between perches (Bautista et al. 2001).

Passerine species have been the most common choice of subjects for tests of general mechanistic and evolutionary/economic models of decision making during foraging (Bateson and Kacelnik 1996; Caraco et al. 1990; Krebs et al. 1978). They have also been a useful model to understand specific problems such as the evolution of aposematic coloration and mimicry in insect prey (Barnett et al. 2007; Rowland et al. 2007).

Some species such as starlings are also agricultural pests; both pure and applied research on these species is therefore important for understanding when they will choose not to eat specific foods and for the development and testing of potential avian repellents (Hile 2004; Hile and Tordoff 2005; Skelhorn and Rowe 2009).

Brain Size and Specialized Cognition

Passerines have provided some important case studies of the independent evolution of large brains (or brain areas) and specialized cognition in nonprimate species. The scatter-hoarding behavior of some parids and corvids has been extensively used to study the relationship between spatial memory and hippocampus size (Smulders 2006), and cowbirds have been used to study the cognitive challenges faced by brood parasites (e.g., Freed-Brown and White 2009; White et al. 2009).

Among the passerines, the corvids stand out due to their large overall brain size; indeed, some authors have suggested that, in terms of their relative forebrain size, they should be considered on a par with nonhuman primates (Emery and Clayton 2004). In addition, a growing number of reports describe cognitive capacities in passerines that were until recently thought to be restricted to humans and great apes. Western scrub jays, for example, show a form of episodic memory, remembering specific information about where and how long ago they hoarded a particular food item (Clayton and Dickinson 1998); they may even show evidence of future planning (Raby et al. 2007). New Caledonian crows and rooks demonstrate sophisticated abilities at using and fashioning tools appropriate for solving specific tasks (Bird and Emery 2009; von Bayern et al. 2009; Weir et al. 2002). Investigators are also discovering that corvids display well-developed social cognition and perhaps even some level of theory of mind (Bugnyar and Kotrschal 2002; Clayton and Emery 2009; Prior et al. 2008).

Seasonality

Passerines living at temperate latitudes breed in a seasonal pattern based on fluctuations in temperature and food availability. In this respect they differ markedly from tropical passerine species such as the zebra finch (an opportunistic breeder), domesticated galliform birds, and common laboratory rodents. Seasonality is associated with profound changes in behavior, physiology, and morphology, resulting in circannual cycles of breeding, molt, and migration. The physiological control of these seasonal changes has been the focus of extensive research on passerines (Ball and Ketterson 2008; Dawson 2008; Hahn et al. 2008). Seasonal aspects of behavior such as song are also associated with volume changes of underlying brain areas (e.g., De Groof et al. 2009).

Development and Individual Differences

Passerines are important model species in studies to understand the interaction of genes and the environment during development, and specifically how resulting individual differences in behavior and physiology affect subsequent fitness (e.g., Muller et al. 2007; Spencer and Verhulst 2007). Birds are useful subjects because both eggs and nestlings are easily accessible for various types of measurement and manipulation (e.g., nutritional, hormonal, or thermal), and fitness can be monitored in the wild using long-term studies of banded nest-box populations (Dingemanse et al. 2004). Great tits (*Parus major*) have been studied in depth to understand the connection between personality traits and fitness (Dingemanse and Reale 2005; Groothuis and Carere 2005). Zebra finch lines bred for different corticosterone levels have provided the first evidence in animals of a connection between personality traits and corticosterone levels (Martins et al. 2007).

Laboratory Husbandry of Passerine Birds

The features of passerines that make them important subjects for research also have implications for their husbandry in the laboratory. These birds differ in many ways from both rodents and galliform bird species. Some features of passerine biology, such as song, flight, and diurnal activity, are common to all members of the group, but others—such as whether a species is a seasonal or an opportunistic breeder, whether it is strongly territorial or colonial, and whether it requires a conspecific tutor for normal song learning—differ between species. Thus although we can make some general statements about appropriate laboratory conditions for passerines, many details will vary depending on the species being studied.

Keeping any bird species in captivity requires careful selection of environmental conditions in order to induce the desired physiology and behavior. As we explain below, many behavior patterns are expressed only if birds receive the correct environmental cues. Appropriate environment can also be important in preventing the development of undesirable abnormal behavior patterns such as compulsive feather pulling, repetitive route tracing, or other stereotypies.

In the following paragraphs we consider the main variables that can be manipulated in captive housing facilities for birds. We discuss how decisions about these variables can affect the birds' physiology and behavior and, as a consequence, both their welfare and the quality of the resulting data. It is not our intention to provide specific husbandry recommendations for individual species, as excellent resources are available (e.g., Hawkins et al. 2001; Hubrecht and Kirkwood 2010; Meaden 1993), but rather to provide a brief overview of some of the salient issues that require consideration.

Origin and Developmental History of Birds

Domesticated species such as zebra finches can either be bought from a breeder or bred in-house. However, as with most wild species, the second option is unlikely to be feasible because many passerines are difficult or impossible to breed in captivity (Meaden 1993). European starlings, for example, lay eggs and incubate them if they have nest boxes in an aviary, but the chicks die within a few days of hatching due to the difficulty of commercially sourcing appropriate food (e.g., tipulid larvae) for the parents to feed the chicks. Passerines intended for research use are usually either hand raised from chicks taken from nests in the wild or caught from the wild as fledged juveniles or adults (Asher and Bateson 2008).

The early postnatal environment can have profound effects on an animal's biology (e.g., Anisman et al. 1998; Pryce and Feldon 2003), suggesting that hand-raised birds might be expected to differ from those raised in the wild or by their own parents. Hand raising is likely to produce animals that are less stressed when confronted with humans during daily husbandry (Hawkins et al. 2003), and indeed there is some evidence that hand-raised parrots are less phobic (Schmid et al. 2006). However, the birds in the latter study were also more aggressive and showed a higher incidence of abnormal and stereotypic behavior (see also Keiper's 1969 findings in hand-raised blue jays, *Cyanocitta cristata*). A correlation between development of abnormal behavior and unnatural raising methods is consistent with zoo data showing that animals raised in the wild show less stereotypic behavior in captivity than those raised in captivity (Mason and Rushen 2006). Preliminary data from our own laboratory on European starlings also show significant differences in the behavior of hand-raised birds and birds caught from the wild as fledged juveniles, suggestive of an altered stress response in these individuals (Feenders and Bateson, submitted).

Early environment is also extremely important in the development of birdsong. Some species, such as the zebra finch, have a sensitive period in which they need exposure to conspecific song in order to acquire normal adult song—zebra finches cannot learn new songs as adults. In comparison, other species, such as the canary and starling, are open-ended learners that can add new songs to their repertoire throughout life (Catchpole and Slater 1995). Thus, to ensure normal adult song, appropriate song tutoring needs to be considered for hand-raised birds.

For all these reasons, researchers should be cautious about the long-term effects of captive and hand raising on the behavior and welfare of captive passerine birds. While it may seem beneficial to captive breed animals in order to reduce their fear of humans, this is unlikely to be the only difference that results. It is important to consider carefully the early development of the study animals when planning a research project.

Housing

Cage Size and Shape

Most captive environments are very unnatural for passerine birds in terms of the amount of space they allow, as even large aviaries do not typically provide space approximating the birds' natural range. Starlings, for example, are estimated to travel up to 20 km a day between feeding and roosting sites (Feare 1984), whereas, according to papers published between 2000 and 2004, the median volume of home cage for this species in the lab was only 0.42 m^3 (Asher and Bateson 2008).

Small cages can elicit abnormal behavior such as stereotypies in starlings and tits (Asher et al. 2009a; Garner et al. 2003a), and have been shown to be associated with the development of pessimistic cognitive biases potentially indicative of a more anxious or depressed state in starlings (Matheson et al. 2008).

Cage shape is another factor that appears to affect the welfare of individually housed starlings—longer cages are associated with fewer stereotypies than taller, shorter cages of the same volume (Asher et al. 2009a). Long cages are probably preferable because they allow greater potential for flight.

Group Size

Whether or not group housing is desirable or even possible varies between species. Social species such as zebra finches, starlings, or warblers are ideally housed in groups in large indoor or outdoor aviaries. In other species, such as magpies, birds can be housed in groups of one male with several females; housing more than one male together may lead to fighting and injuries (personal observation). Some species are territorial during the breeding season but otherwise social, meaning that the potential for group housing may vary with the time of year (or light cycle; see the section below on Photoperiod).

For research purposes it is often necessary to singly house birds. This practice might be optimal for more solitary species (e.g., robins and some tit species) but a source of stress for more social species. Starlings, for example, will forgo foraging success in order to be closer to a group of conspecifics in an adjacent cage (Vasquez and Kacelnik 2000), suggesting that this species strongly values social contact. In singly housed parrots, development of abnormal stereotypic behavior was more common in birds with fewer neighbors, suggesting that isolation might be stressful for this species (Garner et al. 2005).

Enrichment

Whatever the cage size or shape, some form of environmental enrichment should be provided to improve birds' welfare (Young 2003). In starlings, there is evidence that environmental enrichment could be more important than cage size alone in improving welfare indicators (Asher 2007).

Frequently used enrichment items include ropes or natural or artificial branches of differing thickness, natural substrates (e.g., bark or sand) for ground-foraging species, water baths, and areas of cover (nest boxes or foliage). These enrichment stimuli fulfill a number of functions, such as allowing greater use of the space available, promoting performance of natural behavior patterns (e.g., probing behavior in starlings or dust bathing in sparrows), and providing the animals with somewhere to hide. In starlings we have shown that environmental enrichment is associated with fewer abnormal behavior patterns and more optimistic cognitive biases indicative of a more positive affective state (Bateson and Matheson 2007; Matheson et al. 2008). Similarly, tits reduce their stereotypic behavior when moved from small barren cages to an aviary (Garner et al. 2003a). Water baths are likely to be important in many species for feather maintenance; in starlings we found reduced flight maneuverability in birds deprived of water baths (Brilot et al. 2009a). Starlings will pay the cost of having to travel through a heavily weighted door to access a cage equipped with a turf probing tray or protective cover (Asher et al. 2009b), demonstrating the importance this species attaches to these enrichments.

It is essential to monitor the effects of novel enrichment items in cages as they can sometimes have unanticipated negative outcomes; for example, a study on zebra finches found increased fearfulness over time in birds provided with cover in their cages (Collins et al. 2008).

Light

Photoperiod

The diurnal and seasonal behavior of birds is greatly shaped by photoperiod. In temperate-zone photosensitive species such as the starling, both absolute day length and change in day length trigger physiological and behavioral changes associated with breeding and molt (Dawson 2008; Dawson et al. 2001). In the starling, the short days of winter render birds photosensitive such that when days lengthen, the neuroendocrine changes leading to gonadal maturation and breeding are stimulated. Starlings held on 11L:13D retain mature gonads indefinitely. Prolonged exposure (>30 days) to long days results in a photorefactory phase, gonadal regression, and finally molt. In starlings held on 13L:11D the gonads remain regressed indefinitely and the birds never come into breeding condition (Dawson 2007). After a period of long days, photosensitivity in starlings can be reinstated by a period of 25 to 35 days of 8L:16D (Goldsmith et al. 1984). Tropical species, such as zebra finches, are typically kept between 14L:10D and 12L:12D (Hubrecht and Kirkwood 2010). Although day length is likely to be less important in this opportunistically breeding species, there is some evidence that shorter days may increase the proportion of birds breeding (Perfito et al. 2007).

Other seasonal behavior patterns are also susceptible to changes in photoperiod. Night migratory birds, such as many warblers, start being active during the night hours with resting periods during the day if the photoperiod is changed from short days (~8L:16D) to long days (~13L:11D) or vice versa (Wiltschko and Wiltschko 2001). Food-hoarding species such as tufted titmice (*Baeolophus bicolor*) may intensify their hoarding behavior under shortened days (Pravosudov and Grubb 1997).

A change in photoperiod not only influences behavior but also has dramatic effects on the brain. This is best documented in the song system, which increases in volume with increasing photoperiod (Ball and Balthazart 2010; also see the section above on Seasonality).

For all birds housed indoors, the daily transition between light and dark should ideally be gradual in order to allow birds to find a roosting site for the night. Alternatively, a dim nightlight may be appropriate.

Light Quality

Like humans, birds rely heavily on their visual sense. In contrast to humans, however, they can see in the spectral range, including UV (Bennett and Cuthill 1994; Hart 2001; Rajchard 2009). In zebra finches and starlings specific aspects of plumage evident only in UV light are attractive to females and important in mate choice (Bennett et al. 1996, 1997), so mate choice experiments carried out under different illuminations can produce different results. UV light may also have beneficial effects on welfare; juvenile starlings kept under UV-deficient conditions had higher corticosterone levels than birds kept under full-spectrum light (Maddocks et al. 2002).

Potentially important scientific and welfare issues result from the flicker of some artificial light sources such as fluorescent tubes and cathode ray monitors. Birds have a flicker fusion frequency of more than 100 Hz, which is much higher than the 50-60 Hz typical of humans (D'Eath 1998) and means that birds may perceive the flicker of fluorescent lighting and computer monitors. Indeed, it appears that this flicker does affect the birds' behavior. Starlings show different responses in mate choice tests under low- and high-frequency fluorescent lighting, becoming less consistent in their preferences in low-frequency conditions (Evans et al. 2006). Starlings exhibit myoclonus (involuntary muscle twitching) when exposed to fluorescent lighting and cathode ray tube monitors flickering below 150 Hz (Smith et al. 2005a). They are also less active and have higher basal corticosterone levels under low-frequency lighting, suggesting that they may find it more stressful (Smith et al. 2005b).

Finally, there is strong evidence that some passerines can detect the plane of polarized light (mainly natural light in the UV). This cue is thought to be important for orientation during migration (Muheim et al. 2007; Munro and Wiltschko 1995).

Whenever possible, natural light should be used in bird rooms (unless light is the variable under investigation). If natural light is not available, rooms should be lit with high-frequency fluorescent lights that cover the full spectral range. Flickering light sources (including cathode ray monitors) should be avoided in bird housing areas.

Temperature

Temperature is often highly variable in natural environments, changing with both season and time of day. A drop in temperature is often a good predictor of reduced food availability and is likely to be associated with increased energy expenditure. Although temperature often covaries with photoperiod some studies show an independent influence of temperature on behavior. Nonhoarding birds may increase their internal fat deposits and/or increase food intake at low temperatures as a result of greater energy needs (Gosler 2002; Goymann et al. 2006), whereas titmice respond by increasing their food-hoarding behavior (Pravosudov and Grubb 1997). Yellow-eyed juncos (*Junco phaeonotus*) switch from risk-averse to risk-prone foraging decisions at temperatures at which they are unable to defend a positive energy budget (Caraco et al. 1990).

Ambient temperature also influences the dawn chorus of birds. Low overnight temperatures lead to a reduction in chorus intensity and duration (Hutchinson 2002), possibly due to a higher loss of body mass (Thomas and Cuthill 2002). In addition, migratory birds may schedule their migratory activity based on the ambient temperature (Able 1973; Pulido 2007). Finally, temperature seems to be a causal factor in the initiation of breeding, with great tits laying eggs earlier at higher temperatures (Visser et al. 2009).

Humidity

There is a general lack of research into the humidity requirements of passerine birds. Humidity does appear to provide an important cue in opportunistic breeders such as the zebra finch, which starts breeding after drought-breaking rainfall when grass seeds become available (Zann et al. 1995); indeed, one laboratory study showed that a change in humidity alone initiated nest-building behavior in zebra finches (Cynx 2001). More recent research reported that zebra finches kept under constant humidity, temperature, and photoperiod still showed seasonal changes in breeding intensity and behavior (Williamson et al. 2008), but the authors concluded that the birds were probably responding to small, uncontrolled changes in humidity associated with the outside weather. This study illustrates how difficult it is to fully control some important environmental variables in the laboratory.

Food

Due to their high metabolic rates passerines typically specialize in high-energy foods such as fruits, seeds, insects, and meat. However, species differ hugely in diet, with some being relatively omnivorous (e.g., starlings) and others specializing in a particular food type (e.g., manakins, cotingas, and birds of paradise, which are all specialized frugivores). Some passerine species require grit in their diet either to aid the digestion of food (since birds have no teeth) or as a source of calcium and other minerals. To complicate matters, many passerines change their diet from being insectivorous during breeding to frugi- or granivorous at other times of year. It is therefore important to research the diet of a new species carefully before keeping it in captivity.

Feeding regimes during husbandry can influence passerine behavior in a seemingly counterintuitive fashion. Carrying excess fat reserves is costly to birds and probably makes them more vulnerable to predation. As a consequence, birds provided with ad libitum or highly predictable food, and birds that are more dominant, often eat less and carry less fat than birds with a less predictable food supply (Cuthill et al. 2000). Thus low body fat should not necessarily be interpreted as a sign of poor welfare in a passerine bird.

On the other hand, nutrition, especially during early life, has a major impact on behavior in later life and reproductive success. Studies have shown that nutritional stress impairs song development (Brumm et al. 2009; Spencer et al. 2003) and spatial memory (Pravosudov et al. 2005).

Noise

Birds perceive sounds in a different frequency range from humans and laboratory rodents. Whereas humans hear well in the range of 0.2 to 8 kHz, passerines have a narrower range, hearing best in the range of 1 to 5 kHz (Dooling 2002; Heffner 1998). There is no evidence that passerines can perceive infra- or ultrasound (Dooling 2002), so sources of such sound are not a welfare concern for these species. However, raised noise levels are likely to be stressful and cause changes in both physiology and behavior (Cyr et al. 2007; Rich and Romero 2005; Wright et al. 2007). Noise can also directly affect the potential for acoustic communication as birds adapt their songs to environmental noise by changing the frequency, amplitude, and even timing of their songs (Brumm 2004; Fuller et al. 2007; Slabbekoorn and Ripmeester 2008; Warren et al. 2006). Moreover, environmental white noise has been shown to negatively affect the quality of the pair bond in zebra finches (Swaddle and Page 2006).

Husbandry Summary and Conclusions

We have illustrated how a variety of environmental variables can affect the physiology and behavior of passerine birds. Many of the specific examples concern zebra finches and European starlings because of the frequency of use of these species. For many less commonly used species, comparable studies are not available. We hope, however, that our review gives readers a sense of the possible effects of different environmental conditions on passerine bird species. In the absence of explicit recommendations about the most appropriate laboratory conditions for a species, the best approach is for investigators and animal care staff to find out as much as possible about the natural environment and behavior of the species concerned and use this information to guide decisions about laboratory conditions.

The main message that we want to convey is that ill-informed choices about the origins of birds or the conditions in which they are kept in the laboratory can dramatically alter the animals' physiology and behavior. Some of these changes are adaptive responses by the birds to the conditions in which they find themselves; for example, an altered stress response seen as a result of early-life stress could be interpreted as an adaptive response to cues that the environment is tough (Anisman et al. 1998). Similarly, the initiation of reproductive behavior in response to changes in temperature, day length, or humidity is clearly an adaptive response to cues that the season is changing. Some changes in behavior are due to the artificial absence in the laboratory of cues that are normally present in the wild; for example, differences in mate choice between animals in two laboratories could be due to a lack of UV light in one of the facilities. Similarly, a failure of birds to orient correctly in a navigation experiment could be due to the lack of polarized light. Such effects are likely to cause problems for the science the birds are being used for and therefore have implications for the numbers of animals used in research, as more studies will be necessary to understand why the physiology or behavior displayed in one laboratory was not present in another.

Perhaps the more worrisome changes in physiology and behavior are those that result when the bird is unable to respond adaptively to its environment. Examples of potentially maladaptive behavior that we have seen include starlings performing repetitive somersaults in small cages and exhibiting myoclonus under flickering fluorescent light (Asher et al. 2009a; Brilot et al. 2009b; Smith et al 2005a). Abnormal repetitive behavior patterns, such as stereotypies, are inappropriately repetitive in goal or motor pattern, functionless, or self-injurious, and often observed in animals housed in inadequate environments (e.g., Garner et al. 2005; Mason and Rushen 2006). In many cases these behavior patterns are thought to result from thwarted motivations such as an inability to fly, escape, bathe, or engage in normal social behavior. Stereotypies develop over time and become progressively more rigid and more frequent (Mason 1993; Meehan et al. 2004); the latter stages are thought to be associated with irreversible changes in the underlying neural networks, possibly comparable to those seen in autism and schizophrenia (Garner et al. 2003a). Such pathological changes might be associated with a general disinhibition of behavioral control leading to perseveration on a range of cognitive tasks (Garner and Mason 2002; Garner et al. 2003a,b; Vickery and Mason 2005). Supporting the hypothesis that stereotypies might be indicative of psychiatric disorders, stereotypic starlings make more pessimistic judgments, which is a characteristic symptom of depressive disorders in humans (Brilot et al. 2010).

Findings about stereotypies and other abnormal behaviors may be extremely significant given the common use of passerine species in studies of cognition and behavior. A lack of understanding of the potential consequences of an animal's stereotypies could lead researchers to miss an important source of individual variation in performance (Garner 2005). Similarly, myoclonus in humans is a clinical sign often associated with underlying neurological disorders, raising the possibility that starlings with myoclonus could have altered cognition and behavior. Thus, the selection of laboratory conditions that minimize the expression of abnormal behavior patterns is likely to be a significant refinement through its positive impact on animal welfare.

Concluding Remarks

Although passerine birds are rare subjects in laboratory experiments in comparison with other laboratory animals, we estimate that between 151,000 and 215,000 are used worldwide annually in laboratory research. The domesticated zebra finch is the most commonly used species (108 studies published in 2008), but use of wild species such as starlings and house sparrows (together, 47 studies in 2008) is also widespread. Passerines are used mainly in fundamental biological research, including studies of physiology, neurobiology, cognition, and behavior. They offer rich research possibilities not afforded by other species, and are irreplaceable in some areas of research such as the study of birdsong.

Given that so much research on passerines involves behavior, it is crucial to understand the range of factors that can affect how a bird responds. We have presented examples of how behavior can be affected by a bird's genetics (different species have different behavioral phenotypes), its epigenetics (early life experience can induce different phenotypes), and its current environment. Passerine birds have specific needs in the laboratory that require a good understanding of the individual species being used and the scientific question being asked. In many cases good practice for rodents is unlikely to be a useful guide to good practice for passerines, and ill-informed husbandry is likely to result in poor welfare and poor science. Conditions that promote good welfare generally lead to more reliable data, reproducibility, and a reduction in the numbers of animals required by reducing individual variability.

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