Variation in reproductive success across captive populations: methodological differences, potential biases and opportunities

Simon C. Griffith[1], Ondi L. Crino[1], Elizabeth Adkins-Regan[2], Carlos Alonso-Alvarez[3,4], Samuel C. Andrew[1], Ida E. Bailey[5], Stephanie S. Bittner[6], Peri E. Bolton[1], Winnie Boner[7], Neeltje Boogert[8], Ingrid C.A. Boucaud[19], Michael Briga[9], Kate L. Buchanan[10], Barbara A. Caspers[11], Mariusz Cichoń[12], David F. Clayton[13], Sebastien Derégnaucourt[14], Wolfgang Forstmeier[15], Lauren M. Guillette[5], Ian R. Hartley[16], Susan D. Healy[5], Davina L. Hill[7], Marie-Jeanne Holveck[17,18], Laura L. Hurley[1], Malika Ihle[15], E. Tobias Krause[11,19], Mark C. Mainwaring[1,16], Valeria Marasco[7], Mylene M. Mariette[10,20], Meghan. S. Martin-Wintle[21,22], Luke S. C. McCowan[1], Maeve McMahon[13], Pat Monaghan[7], Ruedi G. Nager[7], Marc Naguib[23], Fumiaki Y. Nomano[1], Andreas Nord[24,25], Dominique A. Potvin[26], Nora H. Prior[27], Katharina Riebel[17], Ana A. Romero-Haro[3], Nick J. Royle[28], Joanna Rutkowska[12], Wiebke Schuett[29], John P. Swaddle[30], Michael Tobler[24], Larissa Trompf[1], Claire W. Varian-Ramos[30], Simon Verhulst[9], Clémentine Vignal[21], Avelyne S. Villain[21], Tony D. Williams[31]

[1] Department of Biological sciences, Macquarie University, Sydney, NSW 2109, Australia
[2] Department of Neurobiology and Behaviour, Cornell University, Ithaca, NY 14853, USA
[3] Instituto de Investigación en Recursos Cinegéticos (IREC) – CSIC-UCLM-JCCM, Ronda de Toledo s/n, 13005 Ciudad Real, Spain.
[4] Museo Nacional de Ciencias Naturales - CSIC. Dpt. Ecologia Evolutiva. C/ Jose Gutierrez Abascal 2, 28006 Madrid, Spain.
[5] School of Biology, University of St Andrews, St Andrews, Fife, UK
[6] School of Life Sciences, Arizona State University, Tempe, AZ 85281, USA
[7] Institute of Biodiversity, Animal Health and Comparative Medicine, College of Medical, Veterinary and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK
[8] School of Psychology, University of St Andrews, St Andrews, Fife, UK
[9] Behavioural Biology, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands
[10] School of Life and Environmental Sciences, Deakin University, Geelong, Vic. 3217, Australia
[11] Department of Animal Behaviour, Bielefeld University, PO Box 10 01 33, 33501 Bielefeld, Germany
[12] Institute of Environmental Sciences, Jagiellonian University, Gronostajowa 7, 30-387 Cracow, Poland
[13] Department of Biological and Experimental Psychology, Queen Mary University of London, London E1 4NS, UK
[14] Laboratory Ethology Cognition Development, University Paris West, France
[15] Department of Behavioural Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology, Eberhard Gwinner Straβe 7, DE-82319 Seewiesen, Germany
[16] Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ
[17] Institute of Biology, University of Leiden, Netherlands
[18] Biodiversity Research Centre, Earth and Life Institute, Université Catholique de Louvain (UCL), Louvain-la-Neuve, Belgium
[19] Institute of Animal Welfare and Animal Husbandry, Friedrich-Loeffler-Institut, Doernbergstr. 25-27, 29223 Celle, Germany
[20] Université de Lyon/Saint-Etienne, CNRS UMR 9197 NeuroPSI/ENES, France
[21] Conservation and Research Department, PDXWildlife, 9233 SW Brier Pl, Portland, OR, 97219
[22] Applied Animal Ecology, Institute for Conservation Research, San Diego Zoo Global, 15600 San Pasqual Valley Rd., Escondido, California 92027 USA
[23] Behavioural Ecology Group, Department of Animal Sciences, Wageningen, De Elst 1, 6708 WD Wageningen, The Netherlands
[24] Department of Biology, Lund University, Ecology Building, Sölvegatan 37, SE-223 62 Lund, Sweden
[25] Department of Arctic and Marine Biology, Arctic Animal Biology building, University of Tromsø, NO-9037 Tromsø, Norway
[26] Advanced Facility for Avian Research, University of Western Ontario, London, ON, Canada
[27] Zoology Department, University of British Columbia, Vancouver, BC, Canada
[28] Centre for Ecology and Conservation, University of Exeter, Penryn Campus, TR10 9FE, UK
[29] Zoological Institute, University of Hamburg, Martin-Luther-King Platz 3,20146 Hamburg, Germany
[30] Institute for Integrative Bird Behaviour Studies, Biology Department, The College of William and Mary, Williamsburg, Virginia, USA
[31] Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, Canada, V5A 1S6

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Abstract

Our understanding of fundamental organismal biology has been disproportionately influenced by studies of a relatively small number of ‘model’ species that have been extensively studied in captivity. Laboratory populations of model species are commonly subject to a number of forms of past and current selection that may affect experimental outcomes. Here we examine these processes and their outcomes in one of the most widely used vertebrate species in the laboratory. The zebra finch (*Taeniopygia guttata*) is an important model species for research across a broad range of fields, partly due to the ease with which it can be bred in captivity. However, despite the amenability of zebra finches to captive conditions, we demonstrate extensive variation in the success with which different laboratories and studies bred their subjects, and only 64% of all females that are given the opportunity to breed in the laboratory, do so successfully. We identify and review several environmental, husbandry, life-history, and behavioural factors that potentially contribute to this variation. The variation in reproductive success across individuals could lead to biases in experimental outcomes and drive some of the heterogeneity in outcomes across research groups. From this perspective, research on the captive zebra finch provides a useful case study of the wider problem caused by a failure to provide important contextual information supporting the empirical studies of animals. The zebra finch is an excellent system on which to work in captivity and the aim of this review is to sharpen the insight that future studies of this species can provide, both to our understanding of this species and also with respect to the reproduction of captive animals more widely (important for conservation management). We hope to improve systematic reporting methods and that further investigation of the issues we raise will lead both to advances in our fundamental understanding of avian reproduction as well as to improvements in future welfare and experimental efficiency.

Introduction

There has been a recent call to improve on the reporting of information supporting empirical work conducted on animals to improve evaluation and interpretation, and facilitate the use of data in further work (Kilkenny et al., 2010). In their paper, Kilkenny et al. (2010) outlined the value of capturing contextual information (for example; animal backgrounds, housing and husbandry conditions, sample sizes and selection procedures) with a set of guidelines identifying 20 items that should be addressed in each publication. One of the main underlying drivers of this effort was to reduce the amount of clinical research using laboratory animals (through the UK based National Centre for the Replacement, Refinement and Reduction of Animals in Research). However, in their paper Kilkenny et al., (2010) also highlighted the opportunities that are missed when the context of a particular study is not adequately communicated. Whilst they focused on all animal models, and particularly those used in biomedical research, there were also some clear messages for animal behaviour research. The issues raised by Kilkenny et al. (2010), and related ones outlined below will result in biases in both experimental selection of subjects and evolutionary selection over both long and short time scales. Here we outline these issues by focusing solely on the zebra finch (*Taeniopygia guttata*), although we consider that our central message and recommendations will be more broadly applicable to all species that have already been, or are to be taken, from the wild into the laboratory. The issues that we specifically focus on here are those that arise from the challenge of trying to breed and maintain animals in a way that captures the extent of natural variation seen in wild populations, but in a controlled environment. Our findings are therefore also relevant to those managing and designing captive breeding programs for the benefit of animal conservation (Lees and Wilcken, 2009).

In the wild, we do not expect all individuals in a population of birds to reproduce successfully in a given breeding season or even across a whole lifetime (Newton, 1998). In wild zebra finches the low level of reproductive synchrony across a population (Griffith, Pryke, & Mariette, 2009; Zann, Morton, Jones, & Burley, 1995) suggests that individuals are quite strategic about when they choose to breed. Yet, in two well-monitored populations in the wild, reproductive attempts typically end in failure. For natural nests that are vulnerable to predation, only 11-35% of clutches resulted in fledged young (Griffith et al., 2008a; Zann et al., 1995). Even when predation was reduced through the provision of nest boxes, only 53% of clutches resulted in fledged offspring (Griffith et al., 2008a). The variation in reproductive success in the wild is an interesting question in evolutionary ecology that must ultimately reflect the individual optimisation of many naturally and sexually selected traits. Even in zebra finches that have been brought into captivity, protected from predators, living in standardized environmental conditions, and provided with an *ad libitum* supply of resources, anecdotally many individuals fail to reproduce. Zebra finches are not the exception to the rule, as most individuals brought into captive breeding programs from wild populations fail to reproduce to recruitment (Lees and Wilcken, 2009). This failure presumably reflects some of the same selective pressures to those in the wild as well as additional challenges of living in captivity. Wild animal populations continue to decline at alarming rates (Butchart et al., 2010; Pereira et al., 2010), and captive breeding is becoming an increasingly important tool to guard against extinction in conservation and species management programs. Thus careful evaluation of reproductive failure seen in extensive, multi-institutional captive breeding programs, such as the zebra finch, and other model systems, can provide valuable insight for the planning and design of conservation-focused captive breeding programs (Slade et al., 2014).

As well as being of interest to evolutionary ecologists, the variation in reproductive success among captive birds is worthy of attention due to the importance of the zebra finch as a model system for captive research across a broad range of areas in evolutionary biology, physiology, animal behaviour, neurobiology and genetics (Griffith and Buchanan, 2010; Zann, 1996). One of the reasons it has been so widely adopted as a model species is the relative ease with which it breeds in the laboratory. Zebra finches reach sexual maturity within three months of hatching and adults are capable of reproducing repeatedly, and throughout the entire year under the right conditions of housing and food (Zann 1996). Research scientists and aviculturists recognized it as the easiest songbird to maintain and breed in captivity; often breeding is so robust that it can be stopped only by separating the sexes or by removing all nesting sites. Nevertheless, there is considerable anecdotal evidence that large variation in reproductive success exists among individuals and populations of captive zebra finches. Not all individuals respond similarly when given the opportunity and resources to reproduce: some individuals quickly and repeatedly reproduce regardless of the circumstances, while others fail to reproduce at all over a lifetime in captivity. Although the variance in reproductive success among individuals within a single population has been the explicit target of a small number of studies (e.g. Alonso-Alvarez et al., 2006; Bolund et al., 2009; McCowan et al., 2014), it is much more usually ignored or indeed, leads to removal of those individuals that do not reproduce well either deliberately or inadvertently from populations and experiments alike. Typically studies focused around reproduction report the sample size of pairs that bred and are included in specific analyses and only rarely is a reference is made to additional birds that were given the opportunity but did not lay eggs (e.g. in Gorman et al. 2005, 77% of females produced a clutch). Even among those individuals that initiate a reproductive attempt there is variation in their ability to hatch eggs and rear offspring through to independence. Only rarely is this variation specifically the focus of analysis or comment, even in papers that are focused on aspects of reproductive behaviour or physiology. The variation in these aspects of individual reproductive success in domesticated populations will affect the number of offspring that an individual leaves in subsequent generations. As a result, the underlying determinants of this variation are subject to sexual, natural, and artificial selection. Some of these variables may have been maintained in a fairly constant state for over a hundred generations in captivity and have the potential to cause evolutionary change.

Our aim here is firstly to summarize the extent of variation in the level of reproductive success in domesticated zebra finches across multiple research populations. While these estimates are unsuitable for directly measuring the extent of selection (because they do not represent lifetime reproductive success), they provide a first indication of the extent to which selection might be acting in such populations and the extent to which it may vary between them. The level of contemporary selection is not only important in how it may affect change in various traits across generations, but also in the extent to which it affects the composition of experimental datasets. For example, if there is consistent individual variation in an individual's likelihood of laying eggs after a given number of days (when presented with an opportunity to breed) then the selective pressure will be determined by the amount of time birds are given to breed. For example, as illustrated by a hypothetical situation in Figure 1, an experimental cut-off of 15 days after individuals are given the opportunity to breed will create a systematic bias with respect to a trait that is significantly related to the latency to lay. In this case, most individuals in category 1 will have laid by this time and will be well sampled, while individuals in category 2 will on average start laying later and only half of these birds will have laid by the time of the experimental cut-off. Here the categories might be an ordinal trait such as experience, or a continuous trait such as bill colour divided into two classes. The timescale and the trait itself are illustrative of any situation in which an experimental time point is applied, so that individuals end up separated according to their breeding latency. The bias here will determine the composition of the sample for work focusing on aspects of biology that are measured after the cut-off. For example, if the research focuses on parental care, then the data will be gathered only on the subset of birds that have bred before the experimental cut-off is reached. It will also affect the composition of subsequent generations if the cut-off determines which individuals produce offspring and which do not. There are anecdotal reports that finch breeders only breed females that lay eggs quickly when given a mate, and in the same way this may have affected selection over many generations of domestication. There are many logistical reasons why experimental cut-offs are used and they are probably reasonably widespread. We are not criticising the use of such cut-offs, but raising an awareness of the sort of bias that they may introduce.

The other obvious source of experimental and population bias is where variation in reproductive success is significantly related to variation in traits such as behaviour or morphology (i.e. natural or sexual selection). Such a relationship will result in larger numbers of offspring being produced by a subset of the adult population, affecting the composition of the population over time. It may also result in biases in experimental samples if an outcome requires the production of a certain number of surviving offspring. For example, if the end point of the research project is to compare either sons and daughters, or extra-pair and within-pair offspring that survive to a certain age, then we would be more likely to get data from pairs that produce larger broods. If we can start to develop an awareness of such biases it will help us in the interpretation of results (and variation across studies) and also enable us to control and reduce such bias in future studies.

Our second aim is to review areas of zebra finch biology that might help to explain variation in the extent to which individuals breed and produce recruits in laboratory populations. We believe that these areas offer good opportunities for further exploration and suggest that this might be best done by taking advantage of the many laboratories currently working with this species, through collaborative efforts that provide both variation in and the replication of key variables. Future work could examine sources of variation in reproductive success by controlling for variation across populations while attempting to systematically alter just one or two variables at a time. Given the extensive molecular resources becoming available for this species (Warren et al. 2010), we also have the opportunity to test predictions concerning differences between domesticated and wild populations across a variety of traits that have been subject to directional selection in captivity.

The zebra finch remains an excellent model system with which to conduct work both in the wild and in captivity and we wish to sharpen the insight that future studies of this species can provide. To this end, we highlight the variation that exists across study populations and indicate the potential consequences of biased sampling and breeding. Ultimately, consideration of this variation may provide insight into key traits that have been altered through the process of domestication over the past hundred years.

PART I - The reproductive success of zebra finches in laboratories

Methods – The lead author contacted researchers in North America, Europe, and Australia (the regions where most of the work on captive zebra finches has been done) that have published research on zebra finches in the past ten years to request their involvement in this study. A number of researchers did not respond to this initial communication and are not therefore represented, along with other researchers that were unable to, or did not wish to contribute data on these specific questions. The authors of this paper have contributed their own data where applicable and contributed to the writing of the paper. Data were compiled in an effort to determine the proportion of females that produce a) eggs and b) fledglings, when given the opportunity to breed (Table 1). For these same pairs we also report whether they were housed in a cage or aviary, whether they were force paired or free to choose partners, as well as whether they originated from wild or domestic stock. Contributors provided data from their records, and none of these data were the result of work targeted just at assessing proportional reproductive success. These breeding data were collected as part of researchers' independent on-going research with this species, which was conducted in line with their own animal ethics approvals and the legal requirements of their respective countries. We collated data from situations in which birds were not subject to experimental manipulations that are likely to have significantly affected their reproduction. In cases in which broods had been switched in cross-fostering experimental designs, we used only the data collected up to the point of the cross-fostering. Most of the data we have gathered and presented come from individuals given a single opportunity to breed. However, we have included a focus on one of the studies in which individuals were allowed to breed repeatedly over an extended period of time. The data (provided by Varian-Ramos and Swaddle, from the College of

William & Mary, US, and summarised in Table 2) provide us with an opportunity to assess the repeatability of reproductive success at an individual level. In their study Varian-Ramos et al. (2014) tracked a total of 33 individuals over a twelve-month period in which the birds were allowed to breed *ad libitum*. We used only the data from the control individuals in that study, as those birds were not subject to the experimental treatment that was the focus of that work (Varian-Ramos et al., 2014). Varian-Ramos et al. (2014) removed clutches 21 days after the last laid egg was laid if the eggs failed to hatch, and removed offspring from their parents when they reached independence. One clutch from each pair was removed as part of the study, but all other clutches were left for the parents to hatch and rear. We include these data as they provide important insight into the extent to which reproductive success and failure may be attributable to individual differences.

Statistical methods

Our statistical analyses were focused on addressing individual repeatability of reproductive success, and characterising variation in reproductive success across and within populations, as well as investigating a couple of likely factors that might determine that variation. The percentage of females in each study that succeeded in clutch initiation and producing at least one fledgling in the across-study data set, and the percentage of breeding attempts per female that were successful in producing either fledglings or independent young in the data from the College of William & Mary, US; CW Varian-Ramos and JP Swaddle (Table 2) were transformed into binary data (i.e. 1: success, 0: failure) for all the analyses. Intra-class correlation (ICC) was calculated for this success-failure outcome to examine the variability of reproductive success at the level of study and institution (across-study data), and individual (data from (Varian-Ramos et al., 2014). The ICC in latent scale (link scale) was estimated based on generalized linear mixed models (GLMM) with a binomial distribution with logit link function. Models were fitted to the binary success-failure data. The latent scale ICC serves as a measure of variation in the response variable independent of its mean value, and is comparable across different sets of data (Nakagawa and Schielzeth, 2010). The models included either identity of study, identity of institution, or identity of female as random effects. Effects of these three categorical variables were tested with generalized linear models (GLM). Differences between ICC estimates were examined based on posterior probability. Models were fitted, and parameters were estimated with Markov chain Monte Carlo, using software Stan (http://mc-stan.org/) called from R package rstan (Stan Development Team. 2014).

Across experimental populations the method of assigning mating pairs was either forced pairing or free-choice pairing. The origin of experimental birds also varied between captive breed and wild derived. The effects of these two factors on clutch initiation and fledging success were investigated using GLMM with a binomial distribution and logit link function. In both cases, housing condition (indoor vs. outdoor), pairing type (forced vs. free choice) and origin of strain (captive bred vs. wild derived) were included as fixed effects. Identity of study and identity of institution were included as random effects. Models were fitted using R package lme4 (Bates et al. 2015). Similarly, the effects of female age were examined using GLM with a binomial distribution and logit link function. The difference between females (those who produced at least one fledgling) in the number of fledglings was examined with zero-inflated Poisson model with log and logit link functions using R package pscl (Zeileis et al., 2008).

Results

Individual repeatability in reproductive success

Over a period of continual breeding (52 weeks) 33 females produced 316 clutches (mean = 9.58 ± 2.99 s.d.). In total 1670 eggs were laid (mean clutch size 5.32 ± 1.62 s.d.) and from these eggs 704 chicks hatched (mean per clutch 2.55 ± 1.66 s.d.). From these chicks 544 birds were fledged (mean per clutch 2.00 ± 1.52 s.d.; mean per female 16.48 ± 9.69 s.d.) and 461 independent were produced (mean per clutch 1.82 ± 1.51 s.d.). Overall just 42% of all eggs laid went on to hatch and just 28% of eggs produced an offspring that survived to independence. The correlation between the number of fledglings produced by each female and the number of independent offspring produced was strong ($r^2 = 0.87$, df = 138, t-value = 30.07, $P < 0.001$). However the correlation between the number of hatchlings and fledglings produced was weaker ($r^2 = 0.55$, df = 177, t-value = 14.80, $P < 0.001$), and the correlation between the production of eggs and production of hatchlings was weaker still ($r^2 = 0.088$, df = 314, t-value = 5.51, $P < 0.001$).

Females differed in their likelihood of successfully producing fledglings (likelihood ratio test, $\chi^2 = 171.7$, df = 32, $P < 0.001$, n = 316), in the likelihood of producing independent offspring ($\chi^2 = 159.9$, df = 32, $P < 0.001$, n = 304), and in the number of fledglings produced in successful broods (that produced at least one fledgling; $\chi^2 = 119.54$, df = 32, $P < 0.001$, n = 316 (152 were successful), See Figure 2). The proportion of variation explained by inter-female differences did not differ for the success in rearing young to fledging, and in rearing them to independence (for the production of fledglings, Intra-Class Correlation (ICC) = 0.56, s.e. = 0.095, n = 316 nests; and for independent offspring, ICC = 0.53, s.e. = 0.094, n = 304; posterior probability, Pr(difference < 0) = 0.45).

Cross-study comparison of clutch and fledging success

From Table 1 we combined data from 23 institutions on egg hatching success per female and from 21 institutions on fledgling rearing success per female. In total 2813 females out of 3213 successfully hatched chicks (proportion = 0.88, s.e. = 0.006), and 1899 females out of 2906 raised fledglings (proportion = 0.65, s.e. = 0.01). The probability of females initiating at least one clutch varied across both studies (χ^2 = 378.05, df = 69, P < 0.001, n = 3213) and institutions (χ^2 = 122.37, df = 22, P < 0.01). Similarly, the probability of producing fledglings was different across studies (χ^2 = 575.15, df = 56, P < 0.001, n = 2906, Figure 3) and across institutions (χ^2 = 311.45, df = 20, P < 0.001). Inter-study variation for clutch initiation success (ICC = 0.28, s.e. = 0.049) was higher than inter-institution variation (ICC = 0.12, s.e. = 0.052; Pr(difference < 0) = 0.025, n = 3213 females), suggesting experimental conditions specific to individual studies explains more variation in egg laying than population level factors. The variability of fledging success did not differ between the two levels of grouping (study: ICC = 0.27, s.e. = 0.043; institution: ICC = 0.19, s.e. = 0.061; Pr(difference < 0) = 0.15, n = 2906).

Reproduction and pair and female characteristics

Females were as likely to produce a clutch when housed either indoors or outdoors (Wald test, z = 1.65, P = 0.099, n = 3213 females; Fig. 4a), and when force-paired or given free choice of partner (z = 0.25, P = 0.8), while a higher proportion of females from domestic origin produced a clutch than those from wild (z = -2.08, P = 0.04; Fig. 4b). Females in indoor cages fledged significantly fewer young than did females breeding in outdoor cages (z = 2.42, P = 0.016, n = 2696; Fig. 4c). Females from domesticated strains were more likely to produce fledglings than those in populations derived from the wild more recently (z = -3.65, P < 0.001; Fig. 4d). Females that were force-paired by researchers and pairs formed through mate choice were equally likely to fledge young (z = -0.88, P = 0.38). For three institutions, we could compare success of females from two different age categories (all else is presumed to be equal). In two of the three institutions young females had a greater reproductive success than older ones. In Lund domesticated females (females of 9 versus 20 months) were equally likely to produce a clutch (all females were successful, n = 56), and there was no difference in fledging success (z = 0.106, P = 0.92, n = 56). In domesticated birds in Glasgow (females of 7 versus 43 months) younger females were more likely to produce a clutch (z = 3.57, P < 0.001, n = 144), and to fledge young (z = 5.62, P < 0.001, n = 144). At the Max Planck Institute (Seewiesen) there were comparative age classes across both domesticated and wild derived birds, allowing two separate comparisons. For domesticated birds (1.1 years versus 3.5 years) young birds were more successful at producing clutches (z = -4.214, P < 0.001, n = 328) and in fledging offspring (z = -5.437, P < 0.001, n = 328). For wild-derived birds, (10 versus 24 months) young females also tended to be better at producing clutches (z = -1.028, P = 0.30, n = 114) and fledglings (z = -1.073, P = 0.28, n = 114).

Discussion

We found that a significant percentage (around 35%) of females do not successfully produce offspring when given the opportunity to breed in the captive context. About half of these females fail to produce a clutch, and the remainder were unable to successfully raise offspring. For those females that do produce a clutch, the primary determinant of reproductive failure is hatching failure. However, these birds also fail to raise hatched nestlings to fledging and in the subsequent production of independent young. Some of the overall variation is due to differences across institutions and also across separate studies within institutions. We also found some evidence that the age of females may affect reproductive outcomes, as younger females were more successful than older females in two of three institutions in which there was data available. An important caveat here is that the data that provided the opportunity for the comparison of young and old females did not come from studies that were specifically designed to test that and there are likely to have been other uncontrolled sources of variation. Similarly, whilst not coming from controlled studies designed to test for a difference, we found that females that bred outdoors produced a higher number of fledglings than those that bred indoors although those categories also typically also correlate with the size of the breeding enclosure as birds housed indoors are typically in cages whereas birds housed outdoors are in aviaries.

We also found some evidence for a higher level of reproductive success in domesticated birds than in laboratory populations that were from stock recently derived from wild-caught individuals. This result is consistent with the idea that selection has lead to traits that improve reproductive performance in captive conditions. We found strong evidence of intrinsic variation in individuals' ability to reproduce in the conditions they were provided, as would be required for selection to act. We found moderate intra-class correlation in reproductive success at the level of individual females, across all studies, and individual reproductive success was repeatable in the longitudinal data from the College of William and Mary (Table 2, Figure 2). The latter data also illustrate how strong the selection can be, with a large reproductive skew across the females monitored (although of course some of this may have been due to their mate).

It is important to be mindful that the data presented here were not originally collected in order to address these issues. The heterogeneity in the data sets presented and in the context in which the captive populations were held precludes a comprehensive investigation into the sources of variation in breeding success among these research laboratories. Nevertheless, we believe it is worthwhile to consider and highlight the potential sources of variation that might contribute, at least in part, to variation within and between populations in reproductive success of domesticated zebra finches. Specifically, we discuss: how differences in housing conditions and husbandry practices could contribute to differences in reproductive success between research laboratories; how individual responses to housing conditions can affect variation in reproductive success within laboratory populations; and the effects of variation in reproductive success on genetic diversity in populations of domesticated zebra finches.

PART II – Possible determinants of variation in reproductive success in captive birds

1. Variation in housing conditions and aviculture practices

Many research laboratories keep birds in controlled rooms to remove the confounding effects of temperature, light, and humidity variation on experimental work. Other sources of variation between research laboratories will also include differences in housing conditions and basic husbandry practices. All of these are likely to contribute to variation in reproductive success of domesticated zebra finches. In the wild, zebra finches are opportunistic breeders that use a range of environmental cues to optimize reproductive success (Zann, 1996). In contrast to the generally predictable and primarily photoperiod-dependent development of reproductive systems typical of seasonally breeding passerines (reviewed in Dawson et al. 2001; Sharp 2005), the physiological reproductive axis of zebra finches can respond rapidly to favourable breeding conditions, seemingly at any time of year, despite showing some seasonality to their reproduction (Perfito et al. 2006; Williamson et al. 2008; Zann 1996; reviewed in Hahn et al. 2008). However, individual pairs vary in the timing of breeding in response to these environmental cues, leading to a relatively low level of breeding synchrony within a local population (Griffith et al., 2008b; Mariette and Griffith, 2012a; Zann et al., 1995). This reproductive plasticity means that for domesticated zebra finches even slight variation in housing conditions (e.g. light regime, humidity, food quality, housing density) may have significant repercussions on breeding success. For example, photostimulation affects testes size despite the underlying opportunistic breeding pattern (Bentley et al., 2000). It is generally assumed that zebra finches (as opportunistic breeders) remain at a constant state of breeding readiness given “good” environmental conditions, such as those provided in the laboratory studies, and physiological breeding condition is rarely controlled for. However, field and laboratory studies indicate that individuals are not constantly in a state of breeding readiness, but rather they cycle through breeding and non-breeding periods, which correspond to distinct neuroendocrine states (Perfito et al., 2007; Prior et al., 2013). Even under constant environmental conditions it may be the case that individual zebra finches will regulate their breeding activity and go through periods of breeding rest and may not be physiologically ready to breed when an experiment is started.

Indoor versus outdoor housing

Across studies, there is extensive variation in the basic housing conditions in which breeding birds are kept. For example, some populations of zebra finches are kept in partially outdoor aviaries (e.g. Burley 1986; Gilby et al. 2011; Ihle & Forstmeier 2013) while others experience only indoor conditions (e.g. Gorman & Nager 2003; Birkhead et al. 2006). Outdoor and indoor housing environments probably vary in temperature and humidity (see *Humidity and temperature),* light quality and quantity, as well as other factors that affect the health and well-being of captive breeding birds. For example, in poultry, individuals kept outdoors with direct access to sunlight are better able to synthesise vitamin D resulting in better growth and egg production (Lewis and Gous, 2009). The natural lighting of outdoor housing can also be less stressful for breeding birds compared to the artificial lighting of indoor housing that can cause an increase in glucocorticoid stress hormones (see: *Stress Physiology*; Evans et al. 2012). Artificial lighting may also vary qualitatively across research laboratories depending on the total luminance and whether full daylight spectrum lights are used.

Housing in outdoor aviaries can also have negative effects on health and reproduction. For example, birds housed in outdoor aviaries may have greater exposure to inter-specific transmissions of pathogens resulting in higher levels of disease and morbidity (e.g. Brittingham et al. 1988). Natural weather conditions will be far more variable than indoor conditions, and also vary significantly with the local climate geographically. Extreme or unpredictable conditions (e.g. unexpected cold temperatures) could be stressful for breeding adults and nestlings, resulting in nest abandonment or nestling mortality (Lynn and Kern, 2014). However, of course in the wild weather conditions are also variable and birds should be adapted to dealing with them, and indeed the natural variation may have important stimulatory effects (i.e. light, temperature, humidity).

Outdoor aviaries may also be subject to varying levels of environmental background noise depending on location, and that has adverse effects on reproduction (Barber et al., 2009). It is also possible that indoor locations may also be noisy due to the air handling machinery used. Finally, the type of housing tends to determine the number of birds that are held together (for example, large groups in outdoor aviaries versus small groups in typically smaller indoor cages), which will also potentially confound attempts to understand the effects of indoor versus outdoor housing, for the reasons discussed below.

Housing and social effects

The composition and density of breeding groups of zebra finches is likely to affect both pair bonding and, in turn, reproductive success. In one of the few studies to investigate the affect of breeding density in aviaries Poot et al. (2012) found that birds breeding in lower density conditions produced significantly more and larger offspring. Research in both domesticated (Adkins-Regan and Tomaszycki, 2007; Schweitzer et al., 2014), and wild zebra finches (Mariette and Griffith, 2012c) has focused on the importance of the pair bond in this species for successful reproduction. These studies suggest that pairs that are well acquainted, phenotypically similar to one another, or with a high level of behavioural coordination differ from other pairs in a number of aspects of reproduction such as the time taken to initiate breeding or the number of offspring produced. However, there is variation across studies and in research populations in the way in which individuals can form and maintain pairs. Pairs are either allowed to form naturally in aviaries (free choice – but constrained as individuals become paired and are removed from the mating pool), or are determined by the experimenter as a male and female are placed in a cage together (force-paired; Table 1 and references therein). In the zebra finch, females force-paired to preferred mates laid slightly more eggs or laid the first egg of their clutch sooner, compared to females paired with non-preferred mates (Balzer and Williams, 1998; Holveck and Riebel, 2010). In their recent study, Ihle et al. (2015) found that freely chosen pairs achieved a 37% higher fitness than did experimentally forced pairs. That finding is consistent with recent studies in a number of captive bred zoo species in which animals mated to their preferred partner, rather than to non-preferred or breeding-program assigned partners (often for genetic management), experienced dramatically increased reproductive success (Martin and Shepherdson, 2012).

In addition to the potential stress caused by force-pairing, captive zebra finches also experience stress when separated from their partner during or at the end of experiments (Perez et al., 2012; Remage-Healey et al., 2003; Schweitzer et al., 2014), although some of this stress might have been due to the stress of social isolation itself (i.e. being isolated from other conspecifics). Breeding partners are often separated at the end of experiments and birds are kept in single-sex populations before pairing them at a later date with the same or a different partner for another experiment. In the wild, males and females form enduring partnerships and remain close to one another throughout the year (Mariette and Griffith, 2012c) with little evidence of infidelity (Griffith et al., 2010) or divorce (Zann, 1996), except when they lose a partner to predation or natural mortality. Hence, elevated stress hormones caused by partner separation or forced-pairing could contribute to reduced reproductive success in laboratories (see *Stress physiology*). There is also likely to be an effect on reproduction of the level of experience that a pair have in breeding together (Adkins-

Regan and Tomaszycki, 2007), and yet this is rarely reported or apparently considered methodologically.

The wild zebra finch is a very social bird with individuals nearly always found in the company of small groups of conspecifics (McCowan et al., 2015), and pairs often breeding closely together (Mariette and Griffith, 2012b; Zann, 1996). It is likely that different housing conditions will affect the social conditions under which zebra finches breed in captivity. In aviaries, birds will be free to socially interact with many other individuals, whereas when housed in cages, there is likely to be a reduced degree of visual and acoustic communication between individuals in different pairs (cages). There is some evidence from captive birds that reproductive investment is modified by acoustic signals from other members of a loose social group (Waas et al., 2005). This finding is consistent with the observation that in the wild, despite a low level of synchrony across a whole population, pairs nesting very closely to one another synchronise their reproductive activity (Mariette and Griffith, 2012a). However, whilst social contact can have stimulatory effects on some individuals, there may be inhibitory effects on others (Poot et al., 2012). In the wild, some pairs actively choose to breed alone away from colonies (Mariette and Griffith, 2012a). This may reflect an underlying behavioural polymorphism between social and asocial individuals, with the latter perhaps socially inhibited by the close proximity of others (Dall and Griffith, 2014). Breeding in aviaries, rather than in cages, has the advantage of more closely resembling natural circumstances in which individuals and pairs can act as part of a social network and facilitate each other. However, the social situation in an aviary can create competition for nest sites, nesting material and food, which in turn might result in lower reproductive success for some parts of a population (McCowan et al., 2014).

Variation in the size and construct of social groups (through housing) will also have consequences for the development of social and sexual behaviour in offspring (Mariette et al., 2013; Ruploh et al., 2012). Reproductive success may be affected by the production of song in adults, with key parameters of song structure (complexity, tempo, stereotypy) and output being affected by the environment (Brumm et al., 2009; Holveck et al., 2008) and by the availability of song tutors during early life (Derégnaucourt, 2011). There is some evidence of reduced variance in song structure between wild and domesticated populations (Slater and Clayton, 1991; Woodgate et al., 2012), and it is possible that there is variation in the quality or variance of song across captive populations. Variation in the expression of song across populations may contribute to heterogeneity in reproductive investment and behaviour given the importance of song in stimulating reproduction (Bolund et al., 2012; Riebel, 2009; Woodgate et al., 2012). In addition to affecting the development of song, the early environment also affects the development of song preferences in females (Clayton, 1990a; Honarmand et al., 2015; Riebel et al., 2009), and therefore potentially this may vary systematically across populations.

Humidity and temperature

In wild zebra finches, the trigger of breeding activity has generally been related to rainfall (Zann et al., 1995). Other environmental cues such as humidity and temperature have been shown to both directly (Cynx, 2001; Vleck and Priedkalns, 1985), and indirectly (Williams, 1996a; Williamson et al., 2008) stimulate reproductive behaviour in zebra finches. Variation in humidity could be an informative cue for zebra finches as it is related to rainfall and ground water conditions, which influence both water and food availability. However, humidity is often not accounted for in captive studies and a relatively large range is often considered as constant (Table 1). For example, Williams (1996) considered humidity range of 35-55% as constant. Williamson et al. (2008) found seasonal patterns of maternal investment in birds breeding in 'constant temperature and humidity rooms' but suggest that the 40-60% variation in humidity in their study may have been the variable that could have influenced breeding if the birds are sensitive to such changes. Therefore, it appears important to pay attention to even small changes in humidity, as there remains the possibility that variation in humidity in captive breeding environments may affect reproductive output. Unfortunately, it is very difficult to artificially control humidity to a high degree as air-heating systems typically deliver dry air, and humidity is not often controlled to a high level of precision independently of air temperature.

In addition to humidity, variation in temperature is likely to affect reproductive physiology and behaviour in ways that may contribute to variation in reproductive success. Although wild zebra finches have been recorded breeding throughout the winter in temperatures as low as 2.2°C (Zann et al., 1995), periods of low temperature are associated with a reduction or cessation of reproductive activity (Davies, 1977). Reproductive success in captive birds may be similarly affected by variation in temperature, or across seasons. Captive birds kept at low temperature (7°C) increased food consumption and time to initiate egg laying and decreased the total number of eggs laid (Salvante et al., 2007). Furthermore, presumably due to the costs of thermoregulation, females reduce the amount of heat transferred to eggs during incubation in low temperature conditions (Nord et al., 2010).

Handling and disturbance

Laboratories may vary in a number of standard procedures relating to the provision of cover, the number of times birds are visited during the day, cleaning routines and the type of interaction that birds get from humans, all of which may lead to different levels of disturbance and stress, which may ultimately result in inadvertent selection on stress-tolerant phenotypes. Alternatively perhaps more disturbance simply leads to a higher level of habituation to such factors. To date, there have been few studies investigating these issues in the zebra finch. Collins et al. (2008) found that the provision of a food reward (fresh greens) directly after handling helped birds to recover normal behaviour more quickly after the disturbance. In the same study they also investigated the effect of providing cover (part of the cage was covered with an opaque cloth), but found that this actually increased the level of fearfulness over the course of the experiment (Collins et al., 2008). Although they did not look at reproductive performance in the context of these factors, Collins et al. (2008) found that birds that were rewarded after handling were more attractive when testing in a mate choice assay than those that had not been. The effects of handling or visiting stress on captive animals can be subtle, as seen by significantly different anxiety and pain responses from laboratory rodents in the presence of male versus female research technicians (Sorge et al., 2014).

Diet and nutrition

The basic diet and nutritional supplements provided to breeding zebra finches vary within and across populations and are likely to influence variation in reproductive investment and success (Gorman & Nager, 2003; Monaghan, Metcalfe, & Houston, 1996; Williams, 1996b) and diet effects can be long-lasting and span across generations (Naguib et al., 2006). In Table 1 we have summarised some examples of dietary variation across different studies and populations. It is standard practice to provide zebra finches with an *ad libitum* seed diet, but there can be substantial variation in the quality of food with some diets fortified with vitamins and other supplements. In addition to seed, breeding zebra finches are often supplemented either daily or intermittently with more nutritious foods such as hard-boiled eggs and spinach (Table 1). The diet, often experimentally manipulated, provided to zebra finches prior to and during reproduction can have pervasive effects on reproductive success. For example, females provided with a low quality diet produce smaller eggs, smaller clutches, have lower hatching success, fledge fewer young, and, overall, have lower lifetime reproductive success (Lemon & Barth, 1992; Rutkowska & Cichoń, 2002; Rutstein, Slater, & Graves, 2004; Rutstein, Gilbert, Slater, & Graves, 2004; Selman & Houston, 1996). In males, diet quality can influence bill and plumage coloration, and courtship rate, all of which may then affect female preference and reproductive investment (Atagan and Forst, 2012; Burley et al., 1992; McGraw et al., 2003).

In addition to variation in diet quality, laboratories also vary in the manner in which food is provided to their breeding birds, which could influence reproductive success. For example, the number of outlets through which a given amount of food can be accessed influences the acquisition of that food by individual birds (e.g. Broom & Ruxton 2003; Vahl & Kingma 2007) and large groups of birds in aviaries with a single food dispenser will have to compete much harder than pairs housed in small cages. As a result, in large aviaries, dominant individuals may have greater access to food. Access to food could affect reproductive success by influencing individual decisions about mass regulation (Cuthill et al., 1997), the physiological ability of birds to breed (Rashotte et al., 2001; Sandell et al., 2007), and the expression of condition-dependent sexually selected traits such as bill colour and song rate (Birkhead, Fletcher, & Pellatt, 1998; Pariser, Mariette, & Griffith, 2010).

Overall, we need to remain mindful that the zebra finch is highly opportunistic and is likely to respond to small variations in important environmental parameters such as housing conditions, temperature, humidity, nutrition, and social cues. As such, although many laboratories may attempt to maintain standard conditions of such parameters, variation between and within laboratories is likely to affect reproduction in ways that are currently not accounted for in most studies.

2. Individual responses

Variation in housing conditions and aviculture practices may explain differences in the degree of breeding success of populations of zebra finches *between* laboratories (Table 1). However, variation in breeding success *within* a population of interest is more likely to be driven by individual differences in behavioural and physiological responses to the particular housing, social, and dietary conditions and handling regimes of the population in question. In turn, intra-population variation in physiology and behaviour can be increased by housing practices or decreased due to inadvertent artificial selection (see *Population genetics and artificial selection*). Overall, understanding how individual variation in physiology and behaviour affect reproductive success in captive populations of zebra finches is crucial to teasing apart mechanisms that explain large-scale differences in inter-population reproductive success.

Stress physiology

Individuals can vary substantially in their endocrine responses to environmental stimuli that can, in turn, cause dramatic variation in reproductive behaviours (e.g. Lendvai and Chastel, 2010). For example, in captive zebra finches, some individuals might be more susceptible to stressors associated with housing conditions such as cage conditions, population density, and exposure to caregivers. In birds, stressors activate the hypothalamic-pituitary-adrenal (HPA) axis and result in the release of the steroid hormone corticosterone (reviewed in Cockrem 2013). Corticosterone elicits physiological and behavioural responses that help birds prioritize self-maintenance and survival at the expense of reproduction (reviewed in Wingfield & Sapolsky 2003). Across bird species, corticosterone is associated with delayed clutch initiation (Griffith et al., 2011; Salvante and Williams, 2003), reduced incubation (Edwards et al., 2013; Spencer et al., 2010; Thierry et al., 2013), lower nestling provisioning (Almasi et al., 2008), greater nest abandonment (Spée et al., 2011; Strasser and Heath, 2013), and lower reproductive success (fewer offspring fledged; Schmid et al. 2013). In captive zebra finches, individual variation in stress responsiveness could be a mechanism that explains variation in reproductive success within a population. In this scenario, birds that are least responsive to stressors will have the greatest reproductive success.

Stress responsiveness is both heritable and influenced by the early rearing environment (Adkins-Regan, Banerjee, Correa, & Schweitzer, 2013; Evans, Roberts, Buchanan, & Goldsmith, 2006; Spencer, Evans, & Monaghan, 2009), and even by the stress profile of their partners (Monaghan, Heidinger, D'Alba, Evans, & Spencer, 2012). If birds with low stress responses are more successful at breeding in captivity, this trait will be favoured over time, resulting in captive populations with dampened stress responses. Anecdotally, it is apparent that laboratory populations of birds that are very recently derived from wild birds are much more flighty than domesticated birds (Griffith, Buchanan and Forstmeier pers. obs.). Although not yet systematically explored in zebra finches, physiologically dampened stress responses have been documented in grey partridges (*Perdix perdix*) and white-backed munia (*Lonchura striata*) with wild-derived birds having higher stress responses compared to domesticated congeners (Homberger et al., 2013; Suzuki et al., 2012). Corticosterone has broad pleiotropic effects on physiology and behaviour (Sapolsky, 2000). Inadvertent selection for individuals with low stress responses is likely to have organismal consequences beyond modifications in stress physiology.

Individual and population level HPA axis characteristics may provide a useful way of comparatively testing the deleterious physiological effects of potential sources of reproductive failure as reviewed herein. For example, studies using direct measures of corticosterone can evaluate the relative stress of widespread practices such as forced-pairing (Griffith et al., 2011), mate separation (Perez et al., 2012; Remage-Healey et al., 2003), food restriction (Spencer et al., 2005), and housing conditions such as artificial lighting (Evans et al., 2012; Maddocks, Goldsmith, & Cuthill, 2001). HPA axis characteristics have been used as a tool to diagnose the stressfulness of housing conditions and the efficacy of breeding programs in zoo animals (Scarlata et al., 2012; Shepherdson et al., 2004), the effect of anthropogenic disturbance on reproductive success in free-living birds (Crino et al., 2011, 2013; Müllner et al., 2004; Walker et al., 2005), and the general welfare of captive animals (Fanson et al., 2013; Lane, 2006; Whitham and Wielebnowski, 2013). In summary, identifying the factors associated with housing and experimental procedures that cause stress (as indicated by elevated corticosterone) in breeding zebra finches will allow researchers to mitigate stressful practices and capture reproductive success across a wider range of phenotypes in captive populations, i.e. reducing the strength of selection for ‘stressor-resistant” phenotypes, and the biases that it introduces.

Individual behavioural variation

A recent focus of work in behavioural ecology is the extent to which individuals differ consistently across time and/or context in behaviour (personality) and what selection pressures might maintain this variation (Wolf and Weissing, 2012). There is as yet little information on wild zebra finches, but domesticated zebra finches, like wild birds of other species, vary across personality traits such as boldness, exploratory behaviour, activity, neophobia, and aggressiveness (Beauchamp, 2000; Brust et al., 2013; David and Cézilly, 2011; Martins et al., 2007; Schuett et al., 2011b), raising questions as to how this might directly or indirectly affect mate choice, fertilization success, and/or parental care, and whether sexual selection contributes to maintaining inter-individual variation in personality traits (Schuett et al., 2010).

In breeding zebra finches, personality may influence the speed and willingness with which an individual chooses a mate (David and Cézilly, 2011). Variation in female choosiness may be particularly relevant to variation in reproductive success when males and females are force paired in cages; very choosy females may simply abstain from copulating with the male she is provided (and indeed the same may apply to males). Over time, this could result in inadvertent selection for less choosy females in captive-bred populations (although the percentage of breeding failure in forced pairs in Table 1 suggests that females, despite being selected for generations for high breeding performance, are far from mating indiscriminately). There is as yet a paucity of data comparing mating behaviour of wild and domesticated females (Rutstein, Brazill-Boast, & Griffith, 2007). Comparisons of captive raised and crossfostered individuals from several wild and domesticated populations should help to test whether variation in choosiness is more pronounced on the population or individual level and has changed in captivity, as has been demonstrated in the house mouse *Mus musculus* (Slade et al., 2014).

A more pressing question is whether non-random mate choice with respect to personality contributes to maintaining variation in these traits (Schuett et al., 2010). Both mate preference tests (Schuett et al., 2011b) and experimental pairing of in- and compatible personalities (see for improved reproductive performance e.g. Schuett et al. 2011b) should help answering these questions. In species such as the zebra finch with bi-parental care, mate choice based on assortative mating for personality could moderate sexual conflict in parental care leading to increased reproductive success (Royle et al., 2010). Therefore, pairs with similar personalities may reproduce more successfully because that allows for greater coordination of reproductive and parental behaviours (Schuett et al. 2011b; Mariette & Griffith 2012b; but see Both et al. 2005; Schielzeth et al. 2010; McCowan et al. 2014). Housing practices that limit mate choice (e.g. forced-pairing) could decrease overall reproductive success by preventing individuals from breeding with a complementary personality type.

Conditions experienced by individuals during development can have sustained effects on personality (reviewed in Stamps & Groothuis 2010). Therefore, it is possible that the variation described above in husbandry and housing conditions between laboratories may generate personality variation that affects reproductive success. Unintentional selection for certain personality traits may result from biases in favour of individuals that cope better with captive conditions and breed successfully (McCowan et al., 2014), or those selected to breed or be part of an experiment. The extent to which these biases generally affect experimental outcomes remains to be determined, but could be an illuminating area of future research.

Developmental conditions can also directly affect an individual's mating behaviour and life-history more generally. Zebra finches imprint on visual and song phenotypes (Clayton, 1990b, 1990c; Immelmann, 1972) to an extent that subspecies specific preferences can be easily reversed (reviewed in Clayton, 1990a). Phenotypic quality also affects preferences: individual condition can influence female mate selectivity (Burley and Foster, 2006; Riebel et al., 2009) and also the specific choice of partner, with individuals pairing assortatively (Holveck and Riebel, 2010). The extent of loss of telomere length during early development is correlated with longevity (Heidinger et al., 2012), and it is not hard to imagine that this will also affect an individual's reproductive investment strategy throughout life.

3. Population genetics and artificial selection

Zebra finches were first exported to Europe from Australia in the 1870's for the pet trade (Sossinka, 1970). Since that time, captive-bred zebra finches have been exported to North America and other parts of the world for breeding (Forstmeier et al., 2007; Zann, 1996) where they have subsequently been isolated to an unknown and varying degree at the local, national and continental levels. Domesticated zebra finches used in research in Europe and North America are mostly derived from populations maintained by amateur and professional finch breeders who have bred these populations for over a hundred years without an influx of wild-caught birds from Australia (Zann, 1996). Typically, captive zebra finches have not been bred with the intention of preserving genetic diversity and natural behaviour, because these are not priorities for the amateur and professional aviculturists who maintain most of the zebra finches in captivity (even though some laboratories may manage their stock to optimise these). Finch breeders are partly driven by the creation of new morphs that are selected by line breeding and back crossing, to the extent that there are now 30 recognized colour variants (Zann, 1996). Even ‘wild type’ birds are bred for competitive showing and judged against aesthetics and avicultural standards. As a result of this history, domestic populations may have diverged from their wild congeners, through artificial selection imposed by aviculture, natural selection to captive conditions (Gilligan and Frankham, 2003; Heath et al., 2003), or through genetic drift (Woodworth et al., 2002). Two studies have found morphological differences between wild and domesticated birds, and between different subsets of the domesticated population (Carr and Zann, 1986; Forstmeier et al., 2007). Reassuringly, despite this morphological divergence between populations, however, life-history trade-offs between traits appear very similar between wild and domestic birds held in captivity (Tschirren et al. 2009). Even without intentional selection, the data we present (Table 1) illustrates substantial variation in reproductive success that could contribute to reduced genetic variation and population differentiation across and within laboratory populations.

To date, just a single study has addressed genetic divergence in the domesticated zebra finch. Forstmeier et al. (2007) used microsatellites to analyse 18 captive research populations and 2 wild populations. They found that all captive populations had lower allelic diversity than the two wild populations sampled and many populations showed strong differentiation from one another, particularly between the populations from different continents (Forstmeier et al., 2007). The limited neutral genetic divergence between populations observed by Forstmeier et al. (2007) does not exclude a higher degree of divergence in functional traits across these domestic populations that may determine some part of inter-population variation in reproductive performance. This is clearly an area that will benefit from the application of genomic tools that are becoming so well established in this species (Warren et al., 2010).

Although many researchers work with ‘wild type’ birds, the presence of the colour variants in the background population, or directly in some studies, raises some issues. First, the degree of melanin pigmentation in animals (a likely target of much artificial selection) correlates with various life-history traits (Meunier et al., 2011), through trade-offs associated with the melanocortin system itself (Ducrest et al., 2008), and as a component of behavioural syndromes (Emaresi et al., 2014; McKinnon and Pierotti, 2010). Relatively few studies have specifically examined the effects of colour variants on zebra finch behaviour or physiology, finding effects on sexual imprinting and song learning behaviour (Mann et al., 1991; Vos et al., 1993), and the visual system (Bredenkötter and Bischof, 2003; Eckmeier and Bischof, 2008).

Second, a recent molecular analysis found that white morphs represented a distinct genetic cluster, reflecting their history of selective breeding (Hoffman et al., 2014). In the process of selecting for these colour variants, there may have been unintentional side-effects on other traits, through genetic hitchhiking, selective sweeps, or epistasis. While there have been no investigations of this in the zebra finch, there are examples in other domesticated systems (e.g. rats: Will et al. 2003; Overstreet et al. 2005; dogs: Sutter et al. 2004). The effects of such genetic correlations in the zebra finch might be particularly likely, given that the genome of the domesticated zebra finch consists of few, relatively large linkage blocks compared to other vertebrate genomes (Backström et al., 2010).

Finally, the domesticated zebra finch represents a fragmented population with numerous barriers that reduce the free transfer of genes between different parts of the overall domesticated population across the world. As in small isolated populations in the wild, genetic inbreeding is a problem expected to cause a reduction in reproductive success (e.g. Billing et al., 2012; O'Grady et al., 2006a; Ralls, Ballou, Rideout, & Frankham, 2000). Although Forstmeier et al. (2007) found high heterozygosity within domesticated populations, different levels of inbreeding may still be responsible for variation in reproductive success between laboratories. Accurate genetic pedigrees are probably not available for all birds in most laboratories and for birds sourced from pet shops or finch breeders. As a result, it is difficult to evaluate the extent to which inbreeding effects might contribute to variation in reproductive success amongst different populations or laboratories. However, zebra finches have been used to demonstrate a new method for directly measuring the total amount of realised inbreeding (Knief et al., 2015), opening new opportunities for the study of inbreeding. Biologically, in domestic populations, inbreeding is a selective pressure (Ihle & Forstmeier, 2013). Zebra finches actively avoid mating with familiar siblings (Ihle & Forstmeier, 2013), and full-sibling pairings suffer reduced reproductive success (Bolund et al., 2010). A recent study has also revealed a sensitivity to olfactory cues of kinship, with females reducing reproductive investment when paired with close relatives (Caspers et al., 2015). Furthermore, the effects of inbreeding depression may emerge within a few generations in a small captive population of zebra finches, particularly on sexually selected and morphological traits, and in different populations, deleterious lethal alleles may have been purged out by breeding and previous population bottlenecks (Bolund et al., 2010). As stressful environments can exacerbate the effects of inbreeding (Armbruster and Reed, 2005), housing and other stressors that differ across laboratories might drive variation in the effect of inbreeding depression across different studies. The extent to which inbreeding may be having detrimental effects on reproduction across laboratories remains an open question.

The rapidly reducing costs of population-level genomic analyses will allow future studies to provide insight into the way in which genetic factors and the domestication process may contribute towards variation in reproductive success across laboratories. The assembled zebra finch genome (Warren et al., 2010) provides a scaffold against which we can examine selection and differentiation on functional loci in the genome in comparison with neutral regions (Balakrishnan et al., 2010; Larson and Burger, 2013). Availability of genomic resources will also facilitate the use of genome-wide association studies (GWAS) (e.g. Metzker 2010; Davey et al. 2011; Ekblom & Galindo 2011), and transcriptome sequencing (e.g. Mortazavi et al. 2008; Wang et al. 2009; Ekblom et al. 2014), which will help in the identification of genes responsible for trait differentiation within and between populations. The genetic history of the domesticated zebra finch may be a determining factor underlying some of the variation in reproductive success across different laboratories. However, studies of this highly amenable laboratory model promise to lead the next generation of work in our understanding of functional genomics in birds. In both of these areas there are many exciting opportunities ahead.

4. Conclusions

The ease with which domesticated zebra finches breed in captivity, relative to other birds, have made them a model system for research across a diversity of fields. However, despite the amenability of domesticated zebra finches to captive conditions, we present data here showing a large amount of variation in reproductive success across research laboratories. Although this variation is often noted anecdotally, it has not been the focus of any studies to date. Here, we have highlighted several potential factors that often vary between laboratories that could influence variation in reproductive success in domesticated zebra finches. We accept that there is always likely to be variation in the housing and husbandry practices of different laboratories. Research groups have to make strategic decisions on the basis of space or monetary constraints as well as following different opportunities to optimise local welfare recommendations. Although more standardised conditions across laboratories might be the most desired outcome, at the least we suggest that further consideration should be given to the way heterogeneity in conditions and protocols across different studies may affect outcomes. This may provide insight into why laboratories can find conflicting results when approaching similar questions in the same species (Jennions, 1998; Seguin and Forstmeier, 2012).

Our review of the variation in reproductive success within and across laboratories highlights that studies of the captive zebra finch provide excellent opportunities to understand many aspects of reproductive biology, the sources of variation for fitness, and the mechanisms of the domestication process. We urge authors to bear these issues in mind when interpreting the findings of their studies on this important model species. We also believe that our findings, and future work on the questions we raise in this species, may provide broader insight into the issues that occur when animals are brought into captivity. This is relevant for fundamental animal-based research, but also for the breeding of animals in conservation programs that are increasingly called upon to establish source populations that provide organisms to re-establish or supplement wild populations.

Finally, we endorse the recommendation made by Kilkenny et al. (2010) in their paper outlining the ARRIVE guidelines for the reporting of information that will provide a greater degree of contextual information in a standardized way. Such information will facilitate later attempts to review and analyse variation across studies.

Recommendation

We propose that all future work on captive zebra finches includes the information itemised in Table 4. We suggest that these data could be presented in a Table provided either in the Methods section or as Supplementary material. The information requested in Table 4 is heavily informed by the items outlined in Kilkenny et al.'s (2010) ARRIVE Guidelines and their Table 2 with some additional information that is more relevant to the zebra finch (as discussed above). We advocate that the table be completed and used as is, rather than being modified with fields excluded or additional ones included. A standardised reporting form will facilitate future efforts to harvest and utilise the material presented.

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Figure Legends

Figure 1. This illustrative example (not real data) shows the frequency distribution of the latency to lay after females are given the opportunity to breed. The population is divided into two categories (shaded black and grey). The categories might relate to a nominal trait such as breeding experience together (none or some); age (first year birds or older); or the categorical division of a continuous trait like bill colour. In this example we have illustrated an experimental cut-off at day 15, which if applied would bias the sample in favour of the category of dark-shaded individuals.

Figure 2. Mean number (± s.e.) of fledglings produced per successful brood across 29 females that were given the opportunity to breed repeatedly across a year, and that raised at least some fledglings successfully (7 females failed to fledge any offspring). All 29 females were successful but there are significant differences in how many fledglings they produced (see results). All data were from the longitudinal study by Varian-Ramos et al. (2014).

Figure 3. The proportion of females (± s.e.) that successfully fledged offspring when given the opportunity to breed. Data from 35 studies.

Figure 4. The reproductive output of females when given the opportunity to breed measured through two metrics: producing a clutch (a & b), and producing fledglings (c & d). Females were examined across two categories: either housed indoors or outdoors (a & c); domestic or wild origin (b & d).

Table 1.

Population	**Domestic (D) or Wild derived)**	**Indoor (I) or Outdoor (O)**	**Force paired or free choice[b]**	**N females[a]**	**N weeks given to breed[b]**	**N females produced a clutch**	**N females that produced fledglings**	**Average offspring fledged per successful brood[c]**	**Percentage of females that produced a clutch**	**Percentage of females that produced fledglings[e]**	**Author**
Arizona State University, US	D	I	Free	24	32	17	10	3.60 ± 0.97	71	42	SSB
Bielefeld University, Germany	D	I	Forced	12	10	9	8	2.65 ± 0.99	75	66	BAC
Bielefeld University, Germany	D	I	Forced	15	10	13	8	2.75 ± 0.83	87	53	BAC
Bielefeld University, Germany	D	I	Forced	13	10	13	11	2.82 ± 0.93	100	84	BAC
Bielefeld University, Germany	W	I	Forced	136	20	118	52	3.04 ± 1.15	87	38	ETK,
Bielefeld University, Germany	W	I	Forced	20	16	16	8	2.88 ± 1.55	80	40	ETK,
Bristol University, UK	D	I	Forced	39	12	31	.	.	79	.	KAS KLB
Bristol University, UK	D	I	Forced	35	12	32	.	.	91	.	KAS KLB
Cornell University, US	D	I	Free	36	.	25	.	.	69	.	EA-R
Cornell University, US	D	I	Free	16	.	14	13	3.92 ± 1.44	88	81	EA-R
Cornell University, US	D	I	Free	64	.	.	31	2.68 ± 0.98	.	48	EA-R
Deakin University, Australia	W	O	Free	61	30	53	52	2.93 ± 1.13	87	85	MMM, KB
Deakin University, Australia	W	O	Free	37	7	35	23	2.72 ± 1.33	95	62	MMM, KB
Deakin University, Australia	W	O	Free	21	10	6	5	2.60 ± 0.89	29	24	MMM, KB
Instituto de Investigación en Recursos Cinegéticos, Spain	D	O	Free	41	33	40 in 177 attempts	37 in 137 out of 177 attempts	3.38 ±1.24	98	90	AAR-H, CA-
Instituto de Investigación en Recursos Cinegéticos, Spain	D	O	Free	44	27	42 in 198 attempts	42 in 133 out of 198 attempts	3.48 ± 1.41	95	95	AAR-H, CA-
Instituto de Investigación en Recursos Cinegéticos, Spain	D	I	Forced	78	26	71 in 215 attempts	69 in 146 out of 215 attempts	3.24 ± 1.32	91	89	AAR-H, CA-
Instituto de Investigación en Recursos Cinegéticos, Spain	D	I	Forced	80	15	79 in 98 attempts	74 in 78 out of 98 attempts	4.11 ± 1.39	99	93	AAR-H, CA-
Jagiellonian University, Poland	D	I	Forced	64	8	52	46	3.87 ± 1.18	81	72	MC, JR
Jagiellonian University, Poland	W	I	Forced	39	5	26	3	1.66 ± 0.47	67	8	MC, JR
Lancaster University, UK	D	I	Forced	124	Variable	94	32	3.26 ± 1.21	76	26	MCM, IRH
Lund University, Sweden (Naïve; ca 9 months)	D	I	Forced	11	10	11	8	1.88 ± 0.64	100	73	AN, MT
Lund University, Sweden (Experienced; ca 20 months)	D	I	Forced	45	9.89 ± 2.49	45[g]	32	2.34 ± 1.12	100	71	AN, MT
Lund University, Sweden[h] (Experienced)	D	I	Forced	13	5	12	-	-	92	-	AN, MT
Lund University, Sweden[h] (Naive)	D	I	Forced	10	5	2	-	-	20	-	AN, MT
Macquarie University, Australia	W	O	Forced	40	10	34	21	3.14 ± 1.31	85	53	SCG
Macquarie University, Australia	W	O	Free	29	64	28	17	1.97 ± 0.68	97	59	LT, SCG, MC
Macquarie University, Australia	D	O	Free	23	10	19	13	2.94 ± 1.09	83	56	LCM, SCG
Macquarie University, Australia	D	O	Forced	20	21	20	15	3.11 +/- 1.57	100	75	LH, SCG

(Naïve)											
Macquarie University, Australia	D	I	Forced	28	12	27	19	3.26 +/- 1.28	96	68	LH, SCG
Max Planck Institute for Ornithology, Seewiesen, Germany (Domestic from Amsterdam)	D	I	Forced	56	81 ± 66	44	41	3.69 ± 1.36	79	73	SD
Max Planck Institute for Ornithology, Seewiesen, Germany (Domestic from Sheffield; young females: 1.1yrs)	D	I	Forced	204	30.44 ± 14.61	199	175	2.67 ± 1.28	98	86	WF, MI
Max Planck Institute for Ornithology, Seewiesen, Germany (Domestic from Sheffield; old females: 3.5yrs)	D	I	Forced	124	24.52 ± 8.07	102	72	2.46 ± 1.12	82	58	WF, MI
Max Planck Institute for Ornithology, Seewiesen, Germany (outbred; 2yrs)	W	O	Forced	36	18.48 ± 7.44	31	28	.	86	78	WF, MI
Max Planck Institute for Ornithology, Seewiesen, Germany (outbred; 0.8yrs)	W	O	Free (6:6)	78	13.62 ± 2.78	72	67	2.97 ± 1.45	92	86	WF, MI
Max Planck Institute for Ornithology, Seewiesen, Germany (females inbred: F=0.25; 1.0yrs)	W	O	Free (6:6)	18	13.03 ± 1.88	16	10	2.42 ± 0.96	89	56	WF, MI
Queen Mary University of London, UK	D	I	Free	34	18	33	29	2.86 ± 1.36	97	85	DFC, MM
Queen Mary University of London, UK	D	I	Free	11	8	10	10	3.30 ± 0.95	91	91	DFC, MM
Simon Fraser University, Canada (Experienced)	D		Forced	137	15 days to lay	129	66	3.34 ± 1.58	94	51	TDW
Simon Fraser University, Canada (Naive)	D		Forced	73	15 days to lay	56	29	3.85 ± 1.46	77	54	TDW
University of British Columbia, Canada	D	I	Forced	21	6-12	21	18	3.05 ± 1.76	100	86	NHP
University of Exeter, UK (2007)	D	I	Forced	42	2-3	33	.	.	79	.	WS, NR
University of Exeter, UK (2008)	D	I	Forced	42	12 days to lay	36	.	.	86	.	WS, NR
University of Glasgow, UK (2006, Naïve)	D	I	Forced[j]	26	4 weeks to lay	25	17	3.76 ± 1.44	96	65	DLH, RN
University of Glasgow, UK (2007, Naïve)	D	I	Forced[j]	34	10 weeks to lay	30	13	2.77 ± 1.48	88	45 (N=29; 5 clutches laid on floor were destroyed)	DLH, RN
University of Glasgow, UK (2009, Naïve)	D	I	Forced	38	8 weeks to lay	33	-	-	87	-	DLH, RN

University of Glasgow, UK (age ca 7 months)	D	I	Forced	117	12.87 ± 2.09	116	98	3.28 ± 1.23	99	84	VM, WB, PM
University of Glasgow, UK (age ca 43 months)	D	I	Forced	27	4.12 ± 1.85	19	3	1.67± 1.15	70	11	VM, WB, PM
University of Glasgow, UK	D	I	Forced	101	14	81	65	3.45±1.14	80	64	KAS, PM
University of Groningen, Netherlands	D	I	Forced	351 females in 1255 attempts	7.29 ± 4.38	332 females; 1132 of the 1255 attempts	228 females; 530 of the 1132 attempts with clutch	3.06 ± 1.50	95	65 overall; 42 attempts	MB, SV
University of Groningen, Netherlands	D	O	Free	52	112 ± 72.72	50 in 372 attempts with clutches	50 in 367 out of 372 attempts clutches	3.42 ± 1.79	96	96	MB, SV
University of Groningen, Netherlands	D	I	Forced	43	6	33	32	2.0 ± 1.18	77	74	KAS SV
University of Leiden, Netherlands - 2004	D	I	Forced	30[i]	10	16[k]	.	-	53	-	MJH, KR
University of Leiden, Netherlands - 2005	D	I	Forced	30[i]	10	22[k]	.	-	73	-	MJH, KR
University of Leiden, Netherlands – 2005	D	I	Forced[j]	11	10	11	8	4.00 ± 1.58	100	73	MJH, KR
University of Leiden, Netherlands – 2006	D	I	Forced[j]	13	10	12[k]	5	3.20 ± 1.10	92	38	MJH, KR
University of Lyon/Saint-Etienne, France 2011 (Naïve)	D	I	Free	53	8	30	22	2.45 ± 1.08	57	42	MMM, CV
University of Lyon/Saint-Etienne, France 2012 (Experienced)	D	I	Free	45	8	43	36	2.95 ± 1.31	96	80	ICAB, CV
University of Lyon/Saint-Etienne, France 2013	D	I	Free	14	4	13	.	.	93	.	ICAB, ASV,
University of Lyon/Saint-Etienne, France 2013 (Experienced)	D	I	Free	18	4	15	.	.	83	.	ICAB, ASV,
University of Lyon/Saint-Etienne, France 2013 (Experienced)	D	I	Free	12	4	12	.	.	100	.	ICAB, ASV,
University of Lyon/Saint-Etienne, France 2013 (Experienced)	D	I	Free	12	4	11	.	.	92	.	ICAB, ASV,
University of Montana	D	I	Free	12	31	9	9	4.53 ± 1.20	75	75	OLC
University of St. Andrews, UK	D	I	Forced	24	4	24	13	3.00 ± 1.41	100	54	NB
University of St. Andrews, UK	D	I	Forced	26	10	24	18	3.00 ± 1.14	92	69	LG, IB, SH
University of St. Andrews, UK	D	I	Forced	9	9	7	6	3.33 ± 1.21	78	67	LG, IB, SH
University of St. Andrews, UK	D	I	Forced	10	10	8	8	3.38 ± 1.18	80	80	LG, IB, SH
University of St. Andrews, UK	D	I	Free (12:12)	25	8	24	23	3.57±1.38	96	92	KAS MGE
University of St. Andrews, UK	D	I	Free (12:12)	19	4	19	17	3.06 ± 1.14	100	89	KAS BCT

University of Western Ontario, Canada	D	I	Forced	13	4	10	9	2.75 ± 1.58	77	69	DAP
College of William and Mary, US	D	I	Forced	18	52	18 in 212 attempts	15	1.39 ± 1.99	100	83 overall; 39% of attempts	CVR, JPS

[a] The number of females that were given the opportunity to breed including those that died during the experiment

[b] The number of weeks (roughly) between the establishment of the breeding opportunity and the point when the opportunity/ experiment / data gathering was brought to a close

[c] This is the average number of fledglings per successful brood (i.e. only including broods with at least one fledgling); the standard deviation (SD) refers to the variance between clutches (excluding broods with zero fledglings)

[e] The percentage out of all females given the opportunity

[g] All females produced at least one clutch, but 9 out of the 45 females (20%) produced clutches in which all eggs were infertile

[h] Time from the start of the experiment to clutch initiation differed between experienced (mean = 11.5 ± 2.0 d) and naïve birds (mean = 13.0 ± 3.0 d), as did clutch size (experienced: 4.0 ± 0.25; naïve: 2.0 ± 0.0 eggs). Females, but not males, in the naïve pairs had been housed in outdoors aviaries prior to the experiment. All other birds had been housed indoors.

[i] Females (n=19 and 16 for 2004 and 2005, respectively) for which breeding was unsuccessful after ca. 1 month (no chicks) were given a new male.

[j] Birds first participated in mate preference test, then one male + one female of preferred or non-preferred category were paired

[k] The remaining females (but two) also laid eggs but outside the nest box.

Table 2. Breeding data from 33 females that were given freedom to breed over a twelve month period in cages at the College of William and Mary, US. Eggs were removed 21 days after the last egg was laid if they had failed to hatch. Offspring were removed from their parents once they had reached independence. The data have been ordered by the number of fledglings produced.

Female ID	**No. clutches**	**No. eggs**	**No. chicks**	**No. fledge**	**% eggs hatch**	**% chicks fledge**
99	16	57	0	0	0.0	0.0
121	14	70	5	0	7.1	0.0
300	13	33	0	0	0.0	0.0
1555	14	71	5	0	7.0	0.0
237	15	72	11	7	15.3	63.6
778	4	18	10	7	55.6	70.0
206	13	68	29	11	42.6	37.9
295	9	70	23	11	32.9	47.8
1000	9	29	14	11	48.3	78.6
1744	9	50	17	11	34.0	64.7
1741	10	62	16	12	25.8	75.0
128	11	74	23	13	31.1	56.5
257	8	38	16	13	42.1	81.3
771	6	25	23	13	92.0	56.5
288	14	77	15	14	19.5	93.3
1579	8	68	22	14	32.4	63.6
115	8	39	19	15	48.7	78.9
1825	8	45	18	15	40.0	83.3
1682	11	56	25	16	44.6	64.0
1565	7	30	17	17	56.7	100.0
1941	6	22	20	19	90.9	95.0
264	11	69	26	21	37.7	80.8
218	11	68	26	23	38.2	88.5
198	8	44	24	24	54.5	100.0
254	8	39	30	25	76.9	83.3
1157	7	36	34	25	94.4	73.5
200	6	31	30	25	96.8	83.3
1828	6	30	28	25	93.3	89.3
310	9	47	30	29	63.8	96.7
355	11	74	33	30	44.6	90.9
1561	8	73	40	31	54.8	77.5
1771	7	35	34	33	97.1	97.1
533	11	50	41	34	82.0	82.9

Table 3. An example of the variation in the housing, density, and dietary supplements in recent studies of captive zebra finch.

Institution	Housing	Housing Size (cm)	Density (pairs)	Light	Temp (C)	Humidity (%)	Food Supplement	Reference
Arizona State Univ., US	Cage	39 x 28 x 21	1	14L:10D				Butler et al., (2011)
Cornell Univ., US	Aviary	80 x 190 x100	6-8	14L:10D	22	30-70%	Chopped up hard boiled egg with shells on	Schweitzer et al., (2014)
Univ. Glasgow, UK	Cage	60 x 45 x 40	1	16L:8D	22		Greens, egg	Gorman and Nager (2003)
Lancaster Univ., UK	Cage	120 x 45 x 40	1	16L:8D	20		Egg and vitamins	Mainwaring et al., (2012)
Lund Univ., Sweden	Cage	32 x 48 x 32	1	14L:10D	18-24		Egg food (Witte Molen, the Netherlands), greens	Tobler et al., (2013)
Macquarie Univ., Australia	Aviary	1000 x 800 x 250	20	natural	natural	natural	Sprouted Seed	Gilby et al., (2013)
Max Planck Seewiesen, Germany	Aviary	200 x 500 x 250	1	natural + supplement to 14L:10D	natural	natural	Greens, egg, and vitamins	Ihle et al., (2012)
	Cage	40 × 40 × 40	1	12L:12D				Woodgate et al. (2014)
	Cage	100 x 50 x 50	1	12L:12D			Vitamins, egg food	Derégnaucourt et al., (2012)
Princeton Univ., USA	Cage	55 x 25 x 25	4	8L:16D	21			Perfito et al. (2006)
Sheffield Univ., UK	Cage	50 x 45 x 46	1	14L:10D	~20		Egg, soaked seed	Birkhead et al. (2006b)
Simon Fraser Univ., Canada	Cage	61 x 46 x 41	1	14L:10D	19-23	35-55	Vitamins and egg food	Willie et al. (2010)
	Cage	61 x 46 x 41	1	14L:10D	7-21 (exp range)	75		Salvante et al. (2007)
Univ. California-Davis, USA	Cage	46 x 46 x 46	1	16L:8D	~21	40-70	Egg	Rochester et al., (2008)
St Andrews Univ., UK	Cage	228 × 40 × 40	1	14L:10D	19-22	40-60	Eggs, greens	Williamson et al. (2008)
Groningen Univ., Netherlands	Aviary	320 x 150 x 225	12	natural	natural	natural	Tropical seed mix and fortified canary food	Simons et al. (2012)
Jagiellonian Univ., Poland	Cage	75 × 30 × 40	1	13L:11D	20±2		Egg including the shell, vitamins	Rutkowska et al. (2012)
Bielefeld Univ., Germany	Cage	83 x 30 x 39	1	14L:10D	~24	25	Eggs and soaked seeds (during breeding)	Krause & Naguib (2011)
Instituto de Investigación en Recursos Cinegéticos, Spain	Cage	60 x 40 x 40	1	16L:8D	21-23		Crumbled bread mixed	Romero-Haro & Alonso-Alvarez (2014)
Univ. Exeter, UK	Cage	120 x 45 x 40	1	14.5L:9.5D	19.0		Egg supplement	Schuett et al. (2011a)
Univ. Lyon/ St Etienne, France	Aviary	650 x 550 x 3500	6 – 54	14L:10D	15-30		Egg, salad, vitamins	Mariette et al. (2013)
Univ. Leiden, Netherlands	Cage	80 x 40 x 40	1	13.30L:10.30D	20-22	35-50	Tropical seed mixture, egg food thrice weekly, millet branches twice weekly, germinated seeds once weekly	Holveck & Riebel (2010)

Table 4. A proposed set of data to be completed in all future publications reporting on work focused on the zebra finch.

Aspect	Item	Detail
Study Design	N experimental groups	
	N control groups	
	Nature of replication	e.g. whole experiment was conducted twice
Numbers used	N adult males used	(count all individuals that were initially used)
	N adult females used	
	N males with opportunity to reproduce	
	N females with opportunity to reproduce	
	N females that laid eggs	
	N females that had chicks	
	N females that fledged young	
	N males for which data is presented	
	N females for which data is presented	
	N individuals that died or removed	e.g. one bird was removed after injuring a wing
	Other reasons for missing data	e.g. some blood samples not assayed
Experimental Procedures	Nature of any experimental manipulation	Specify details (i.e. testosterone implant)
	Nature of any invasive work	e.g. 30µl blood sample during chick rearing
	Duration given for breeding opportunity	e.g. in weeks
Experimental Animals	Domesticated or wild stock	Domesticated or recent Wild origin
	Source population	Recent origin of stock (i.e. UK domestic birds)
	Variety	wild type plumage or colour morph
	Age	less than a year, or greater than a year, or mix
	Average mass of adults	mass in g
	Prior Breeding experience	yes/ no (or mix)
	Allocation of breeding partners	e.g. force paired or free choice
	Any bias in selection of individuals	e.g. only birds with breeding experience used
Housing and husbandry	Cage/ aviary size	width x breadth x height (m)
	N individuals per cage	
	Sex ratio present in each cage	e.g. 0.5 (as many males as females)
	Food provided ad libitum	e.g. dry seed finch mix
	Supplemental food provided	type and frequency
	Any restriction in provision of food	e.g. seed provided mixed with husk
	Type of nest site provided	e.g. wooden nest box, woven basket
	Nesting material provided	e.g. Hessian fibre, coconut fibre, feathers, grass
	Environmental enrichment or shelter	e.g. shelter in 1/3 of cage
	Indoors or outside	
	Temperature control	e.g. constant 25 degrees, or local outside conditions
	Humidity control	e.g. 50%
	Light/ dark cycle	e.g. 14L :10D
Results - baseline data	Average clutch size	mean ± standard deviation
	Average number of fledglings	mean ± standard deviation (excluding zeros)

Figure 1

1525

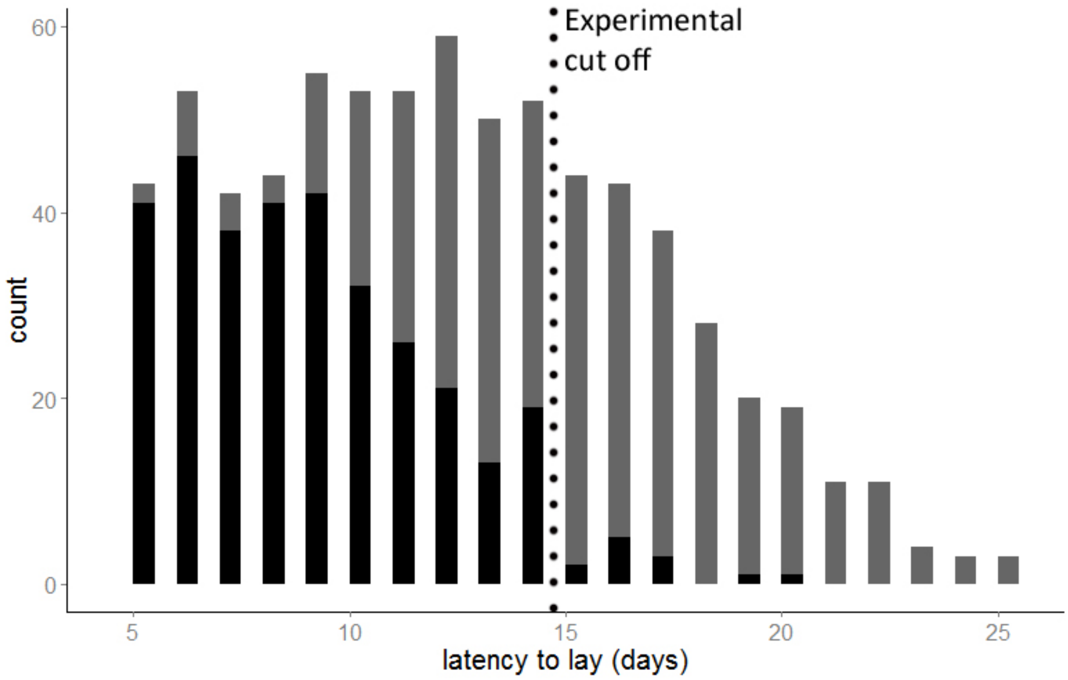
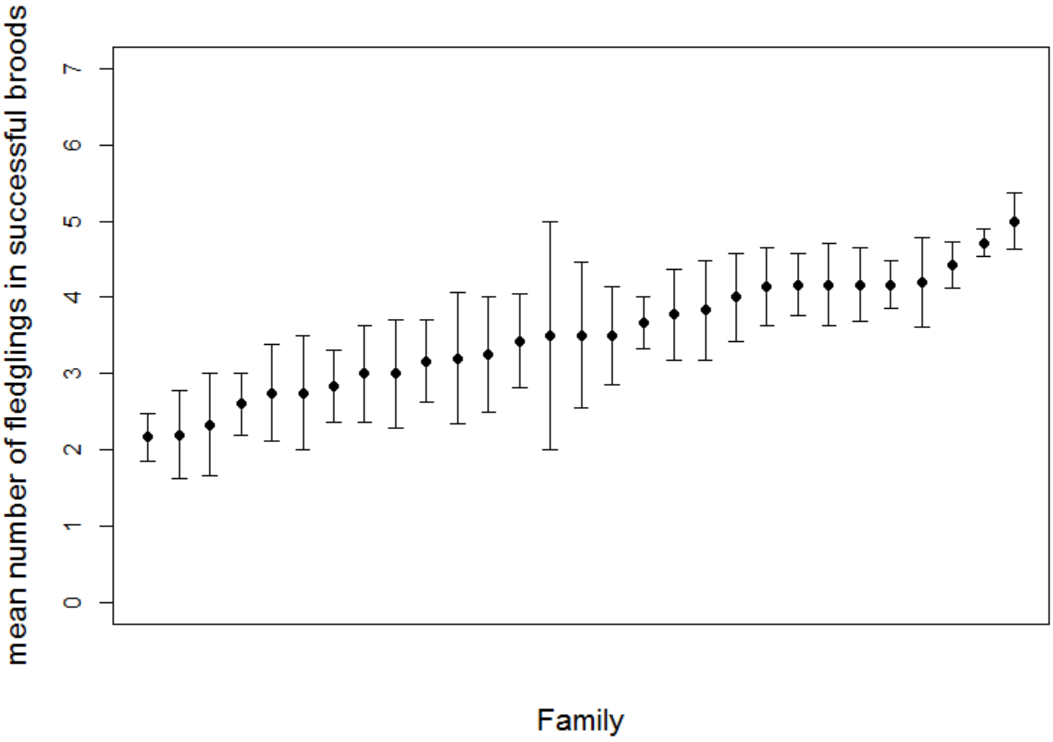


Figure 2.


mean number of fledglings in successful broods
0
1
2
3
4
5
6
7
Family

1540 Figure 3.

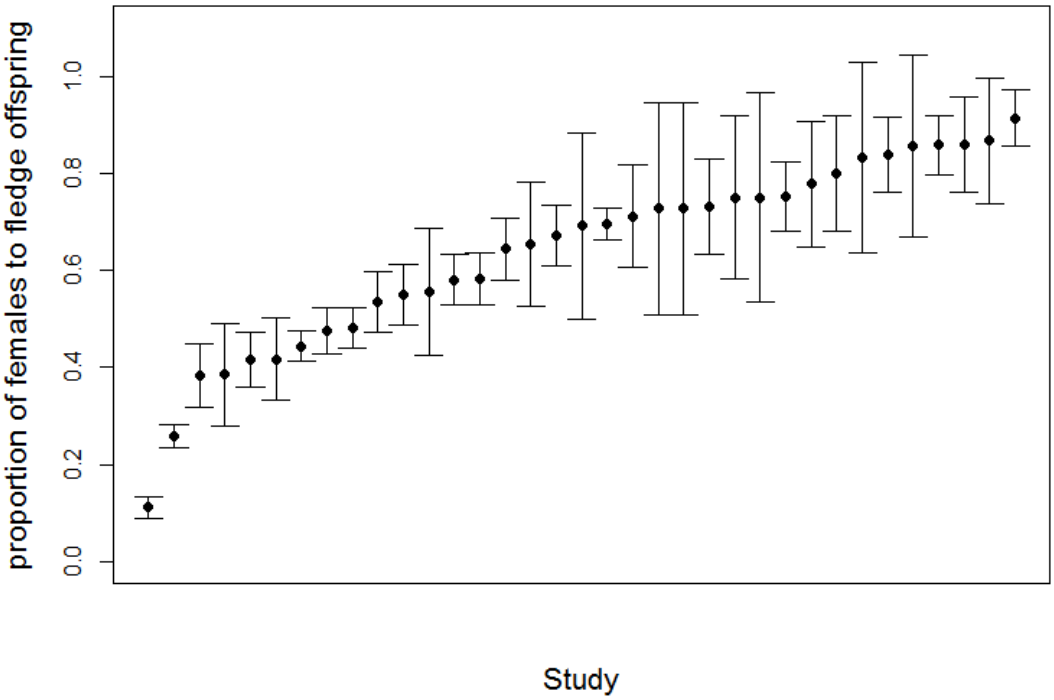
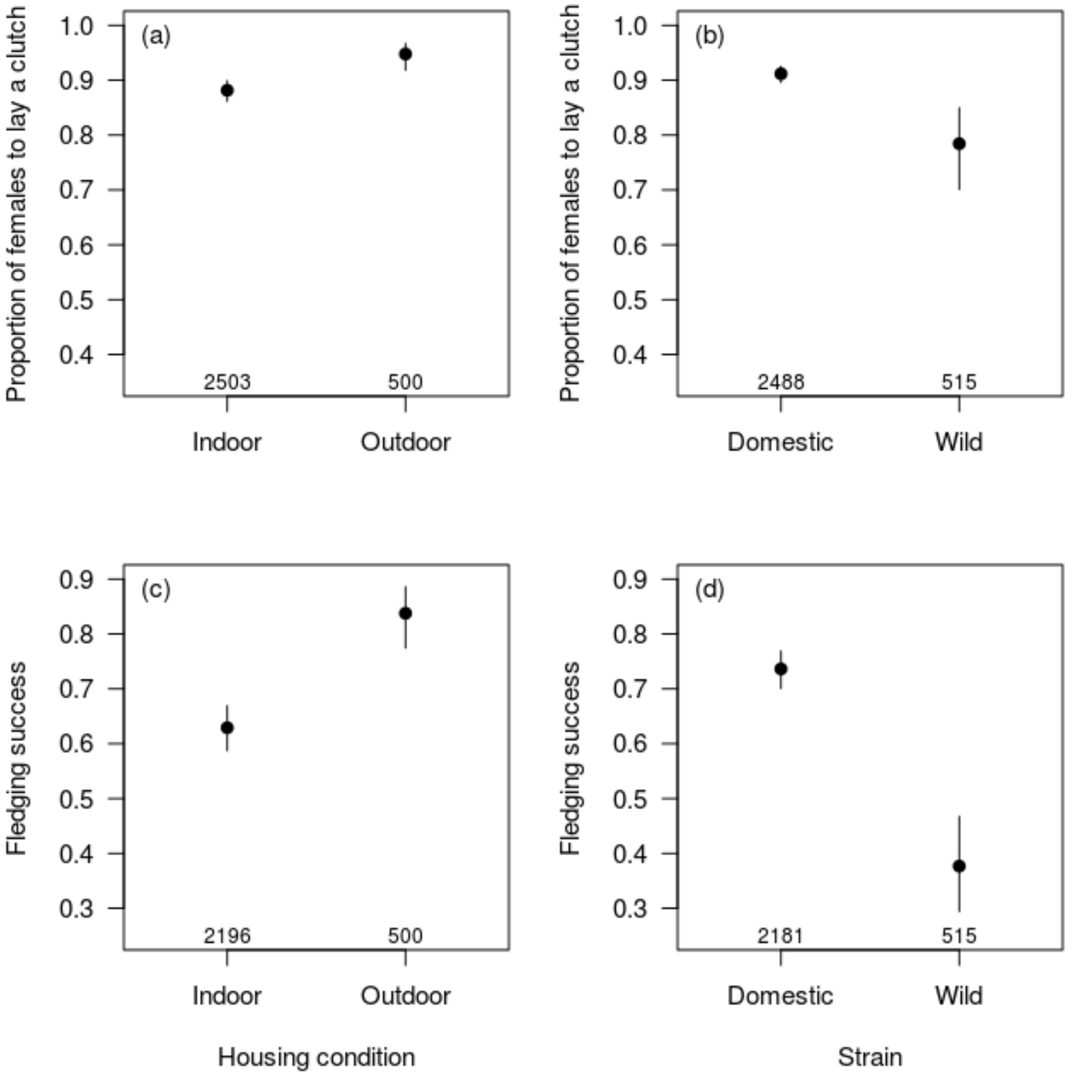


Figure 4.


(a)
(b)
(c)
(d)
Proportion of females to lay a clutch
Fledging success
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
2503
500
2488
515
2196
500
2181
515
Indoor
Outdoor
Domestic
Wild
Housing condition
Strain