

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

- 5 Simon C. Griffith¹, Ondi L. Crino¹, Elizabeth Adkins-Regan², Carlos Alonso-Alvarez^{3,4}, Samuel C. Andrew¹, Ida E. Bailey⁵, Stephanie S. Bittner⁶, Peri E. Bolton¹, Winnie Boner⁷, Neeltje Boogert⁸, Ingrid C.A. Boucaud¹⁹, Michael Briga⁹, Kate L. Buchanan¹⁰, Barbara A. Caspers¹¹, Mariusz Cichoń¹², David F. Clayton¹³, Sebastien Derégnaucourt¹⁴, Wolfgang Forstmeier¹⁵, Lauren Guillette⁵, Ian R. Hartley¹⁶, Susan D. Healy⁵, Davina L. Hill⁷, Marie-Jeanne Holveck^{17,18}, Laura L. Hurley¹, Malika Ihle¹⁵, E. Tobias Krause¹¹, Mark C. Mainwaring^{1,16}, Valeria Marasco⁷, Mylene M. Mariette^{10,19}, Meghan. S. Martin-Wintle^{20,21}, Luke S. C. McCowan¹, Maeve McMahon¹³, Pat Monaghan⁷, Ruedi G. Nager⁷, Marc Naguib²², Fumiaki Y. Nomano¹, Andreas Nord^{23,24}, Dominique A. Potvin²⁵, Nora H. Prior²⁶, Katharina Riebel¹⁷, Ana A. Romero-Haro³, Nick J. Royle²⁷, Joanna Rutkowska¹², Wiebke Schuett²⁸,
10 John P. Swaddle²⁹, Michael Tobler²¹, Larissa Trompf¹, Claire W. Varian-Ramos²⁹, Simon Verhulst⁹, Clementine Vignal¹⁹, Avelyne S. Villain¹⁹, Tony D. Williams³⁰

¹Department of Biological sciences, Macquarie University, Sydney, NSW 2109, Australia

²Department of Neurobiology and Behaviour, Cornell University, Ithaca, NY 14853, USA

- 20 ³Instituto 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. Ecología Evolutiva. C/ Jose Gutierrez Abascal 2, 28006 Madrid, Spain.

⁵ School of Biology, University of St Andrews, St Andrews, Fife, UK

- 25 ⁶School 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

- 30 ⁹Behavioural Biology, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

¹⁰School of Life and Environmental Sciences, Deakin University, Geelong, Vic. 3217, Australia

¹¹Department of Animal Behaviour, Bielefeld University, PO Box 10 01 33, 33501 Bielefeld, Germany

¹²Institute 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

- 35 ¹⁴ Laboratory Ethology Cognition Development, University Paris West, France

¹⁵ Department of Behavioural Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology, Eberhard Gwinner Straße 7, DE-82319 Seewiesen, Germany

¹⁶Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ

¹⁷ Institute of Biology, University of Leiden, Netherlands

- 40 ¹⁸ Biodiversity Research Centre, Earth and Life Institute, Université Catholique de Louvain (UCL), Louvain-la-Neuve, Belgium

¹⁹ Université de Lyon/Saint-Etienne, CNRS UMR 9197 NeuroPSI/ENES, France

²⁰ Conservation and Research Department, PDXWildlife, 9233 SW Brier Pl, Portland, OR, 97219

- 45 ²¹ Applied Animal Ecology, Institute for Conservation Research, San Diego Zoo Global, 15600 San Pasqual Valley Rd., Escondido, California 92027 USA

²² Behavioural Ecology Group, Department of Animal Sciences, Wageningen, De Elst 1, 6708 WD Wageningen, The Netherlands

²³ Department of Biology, Lund University, Ecology Building, Sölvegatan 37, SE-223 62 Lund, Sweden

- 50 ²⁴ Department of Arctic and Marine Biology, Arktisk biologibygget, University of Tromsø, NO 9037 Tromsø, Norway

²⁵ Advanced Facility for Avian Research, University of Western Ontario, London, ON, Canada

²⁶ Zoology Department, University of British Columbia, Vancouver, BC, Canada

²⁷ Centre for Ecology and Conservation, University of Exeter, Penryn Campus, TR10 9FE, UK

- 55 ²⁸ Zoological Institute and Museum, University of Hamburg, Martin-Luther-King Platz 3, 20146 Hamburg, Germany

²⁹ Institute for Integrative Bird Behaviour Studies, Biology Department, The College of William and Mary, Williamsburg, Virginia, USA

³⁰ Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, Canada, V5A 1S6

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65 **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 they 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, do so successfully. We identify and review several environmental, husbandry life-history and behavioural factors that are potentially contributing 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 with which to conduct 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 further investigation of the issues we raise which will lead to advances in our fundamental understanding of avian reproduction as well as improving 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, Browne, Cuthill, Emerson, & Altman, 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, 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 their paper focused on all animal models, and particularly those used in biomedical research, there are also some clear messages for animal behaviour research. Furthermore, we believe that from the perspective of evolutionary biology, there are additional reasons for adhering to Kilkenny et al.'s (2010) recommendations as a result of biases in both experimental selection of subjects and evolutionary selection over both long and short time scales. Here we outline these issues by focusing singularly on the zebra finch, but believe that our central message and recommendations are more broadly applicable to all species which have already been, or are to be taken from the wild into the laboratory as the focus of work over an extended period of time, including multiple generations. The issues that we are specifically focused on are those that arise from the challenge of breeding and maintaining animals in a way that captures the extent of natural variation as 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.

In the wild, we do not expect all individuals in a population of birds to
120 successfully reproduce 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.
Still, in two well-monitored populations in the wild, reproductive attempts typically
125 end in failure. For natural nests that are vulnerable to predation, only 11-35% of
clutches resulted in fledged young (Griffith et al., 2009; 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., 2009). The variation in
reproductive success in the wild is an interesting question in evolutionary ecology that
130 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 comfortable environmental conditions, provided with an *ad
libitum* supply of resources, many individuals fail to reproduce. Zebra finches are not
the exception to the rule, most individuals brought into captive breeding programs
135 from wild populations fail to reproduce to replacement (Lees & 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
conservation breeding is becoming an increasingly important tool to guard against
140 extinction. 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 (e.g. Slade et al. 2014).

The variation in reproductive success among captive birds is also interesting
145 from an evolutionary ecology perspective, but is additionally worthy of attention due
to the importance of the zebra finch as a model system for captive research. The zebra
finch is a model species for research across a broad range of areas in evolutionary
biology, physiology, animal behaviour, neurobiology and genetics (Griffith &
Buchanan, 2010; Zann, 1996). One of the reasons it has been so widely adopted as a
150 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
155 it can only be stopped by separating the sexes or 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 respond similarly when given the opportunity and resources to
reproduce. While some individuals quickly and repeatedly reproduce regardless of the
160 circumstances, others fail to reproduce at all over a lifetime in captivity. 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). However, this variation is largely ignored and
individuals that do not reproduce well are either deliberately or inadvertently selected
165 out of populations and experiments alike. Typically studies focused around
reproduction will report the sample size of pairs that bred and are included in specific

analyses. Sometimes 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), but more often studies report on the pairs that bred but make no mention of
170 any additional birds. 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
175 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.

180 Our aim 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 will not represent lifetime reproductive success), they will provide a first indication of the extent to which selection might be acting in such
185 populations and the extent to which it will vary between them. The level of contemporary selection is not only important in how it may affect change across generations in various traits, but also through the extent to which it will affect 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
190 (when presented with an opportunity to breed) then the selective pressure will be determined by the amount of time that investigators give birds in which to breed. For

example as illustrated by a hypothetical situation in Figure 1, an experimental cut-off 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, individuals in category 1 will have mostly 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 just 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 after the cut-off. For example, if the research focuses on parental care, then the data will only be gathered 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 quickly lay eggs when given a male to breed with, 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 biases 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 research is to compare either sons and daughters, or extrapair and within-pair offspring that survive to a certain age
220 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
225 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 and the replication of key variables. Future work could
230 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
235 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 the aim of this review is to sharpen the insight that future studies of this species can provide. To this end, our review highlights the variation that exists across study populations and indicates the potential biases that
240 may occur as a result 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. We believe it is important to draw attention to the fact that experimental outcomes in this species may arise from the different environments in which they are conducted (e.g. Rojas Mora &

245 Forstmeier 2014).

PART I - The reproductive success of zebra finches in laboratories

Methods – We contacted laboratories in North America, Europe and Australia that have published research focused on zebra finches in the past ten years to request their

250 involvement in this study. From those laboratories that responded positively, data were compiled in an effort to address the following: what proportion of females produce a) eggs and b) fledglings, when given the opportunity to breed? For these same pairs we also report whether they were in a cage or aviary, whether they were force paired or free to choose partners, as well as whether they originated from wild
255 stock or domestic stock. Contributors provided data from their records, and none of this data was the result of work targeted just to assess proportional reproductive success. This breeding data was collected as part of researchers' independent on-going research with this species and was conducted in line with their own animal ethics approvals and the legal requirements of their respective countries. We collated
260 data from situations in which birds were not subject to experimental manipulations that would have significantly affected reproduction. In some cases, broods were switched in cross-fostering experimental designs and we only used the data collected up to the point of the cross-fostering. A number of laboratories that have conducted work on zebra finches did not respond to our initial emailed communication and are
265 therefore not represented, along with other laboratories that were unable to contribute data on these specific questions. Most of the data we have gathered and presented

focused on a set of individuals given a single opportunity to breed. However a couple of studies had allowed individuals to breed repeatedly over an extended period of time. The data provided by Varian-Ramos and Swaddle (from William & Mary College, US, and summarised in Table 2), provides 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 they were allowed to breed ad libitum. The data used here is just from the control individuals in their study, that were not given the experimental treatment that is the focus of that work (Varian-Ramos et al 2014). In their study, clutches were removed 21 days after the last laid egg was laid if they failed to hatch, and offspring were removed from their parents when they reached independence. One clutch from each pair was removed as part of their study, but all other clutches were left for the parents to hatch and rear. This data provides important insight into the extent to which reproductive success and failure may be attributable to individual differences.

Statistical methods

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 William & Mary College, US; CW Varian-Ramos and JP Swaddle (Table 1) 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
295 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 & Schielzeth 2010).
300 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 of difference (Bayesian P value). Models were fitted, and parameters were estimated with Markov chain Monte Carlo, using software Stan
305 (<http://mc-stan.org/>) called from R package rstan (Stan Development Team. 2014).

Across experimental populations the method of assigning mating pairs differed between either force-paired or free choice pairs. 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
310 distribution and logit link function. In both cases, pairing type (forced vs. free choice) and origin of strain (domestic vs. wild) 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, and the
315 difference between females (those who produced at least one fledgling) in the number of fledglings was examined with GLM with a Poisson distribution and log link function.

Results

320 *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.; 325 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 nestlings and fledglings 330 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 335 (likelihood ratio test, $\chi^2 = 171.7$, $df = 1$, $P < 0.001$, $n = 316$); in the likelihood of producing independent offspring ($\chi^2 = 159.9$, $df = 1$, $P < 0.001$, $n = 304$); and also in the number of fledglings produced in successful broods (that produced at least one fledgling; $\chi^2 < 24.57$, $df = 1$, $P < 0.001$, $n = 152$, See Figure 2). The proportion of variation explained by inter-female differences was similar for the success in rearing 340 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; Bayesian P value, Pr (difference < 0) = 0.45).

345 *Cross-study comparison of clutch and fledging success*

From Table 1 we combined data from 23 institutions that provided data on egg hatching success per female and 21 institutions that provided fledgling rearing success per female. In total 2813 females out of 3213 successfully hatched chicks (proportion = 0.852, s.e. = 0.002), and 1889 females out of 2906 raised fledglings (proportion = 350 0.642, s.e. = 0.003). The probability of females initiating at least one clutch varied across both studies ($\chi^2 = 5.12$, df = 1, P = 0.02, n = 3213) and institutions ($\chi^2 = 122.37$, df = 1, P < 0.01). Similarly, the probability of producing fledglings was different across studies ($\chi^2 = 13.36$, df = 1, P < 0.01, n = 2906) and across institutions ($\chi^2 = 325.9$, df = 1, P < 0.01, Figure 3). Inter-study variation for clutch initiation success 355 (ICC = 0.28, s.e. = 0.055) was higher than inter-institution variation (ICC = 0.11, s.e. = 0.043; Pr (difference < 0) = 0.005, 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 was similar between the two levels of grouping (study: ICC = 0.27, s.e. = 0.04; institution: ICC = 0.19, s.e. = 360 0.06; Pr (difference < 0) = 0.14, n = 2906).

Reproduction and pair and female characteristics

Females were as likely to produce a clutch when force-paired or given free choice of partner (Wald test, z = 0.64, P = 0.52, n = 2885 females; Fig. 4a), and when from wild 365 or domestic origin (z = -1.32, P = 0.19; Fig. 4b). In contrast, the proportion of females that produced fledglings was higher in domesticated strains than populations derived

from the wild more recently ($z = 2.3$, $P = 0.021$, $n = 2578$; Fig. 4c). Females that were force-paired by researchers had a lower fledging success than pairs formed through mate choice ($z = -2.5$, $P = 0.011$; Fig. 4d). For three institutions, females from two
370 different age categories were bred and the classes could be compared (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 (females of 9 versus 20 months) females 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
375 Glasgow (females of 7 versus 43 months) younger females were more likely to produce a clutch ($z = 3.57$, $P < 0.001$, $N = 1296$), and produce fledglings ($z = 5.62$, $P < 0.001$, $N = 1296$). At the Max Planck (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 had
380 greater success at producing clutches ($z = -4.214$, $P < 0.001$, $N = 328$) and fledging offspring ($z = -5.437$, $P < 0.001$, $N = 328$). For wild derived birds, (10 versus 24 months) young females were also better at producing clutches ($z = -1.028$, $P = 0.30$, $N = 114$) and fledglings ($z = -1.073$, $P = 0.28$, $N = 114$).

385 **Discussion**

The data presented and the analysis conducted indicate that a significant percentage (around 35%) of females do not successfully produce offspring when given the opportunity to breed in these captive studies. This reproductive failure is partly due to the failure of about half of these females to produce a clutch. For the remainder of
390 females that produce a clutch, the primary determinant of reproductive failure is the ability to successfully hatch their eggs. However there is also failure to raise hatched

nestlings into fledglings and a much lower level of failure between fledging and the production of independent young. Some of the overall variation is determined by differences across institutions and also across separate studies within institutions. We
395 also found strong evidence that the age of females is important in reproductive outcomes, with younger females being more successful than older ones. In addition, we found evidence that females that were free to choose their own partner were more successful than those to whom a partner had been assigned (force-paired), in line with a recent study that found free choosing females to have a 37% higher level of
400 reproductive success (Ihle et al 2015).

Whilst the sample size was limited and there may be other confounding factors, we also detected 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
405 selection has occurred, favouring 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
410 was found to be repeatable in the longitudinal data from William and Mary College (Table 2, Figure 2). The latter data also illustrates how strong the selection is likely to be, with a large reproductive skew across the females monitored (although of course some of this may have been due to the male they were paired with).

It is important to be mindful that the data presented here were not collected
415 systematically to address these issues. The heterogeneity in the data sets presented, and the context in which the captive populations were held sensibly 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
420 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
425 variation in reproductive success on genetic diversity in populations of domesticated zebra finches.

PART II – Determinants of reproductive success in captive birds

1. Variation in housing conditions and aviculture practices

430 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
435 finches are opportunistic breeders that use a range of environmental cues to optimize reproductive success. 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 reproductive axis of zebra finches is able to rapidly adapt to favourable breeding conditions –
440 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). This breeding strategy has important bearing on domesticated zebra finches because slight variation in housing conditions (e.g. light regime, humidity, food quality, housing density) may have broad repercussions on breeding success. For
445 example, photostimulation does affect testes size despite the opportunistic breeding pattern widely observed (Bentley, Spar, MacDougall-Shackleton, Hahn, & Ball, 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 breeding condition is rarely controlled
450 for. However, field and laboratory studies indicate that individuals are not at a constant of breeding readiness, cycle through breeding and non-breeding periods, which correspond with distinct neuroendocrine states (Perfito, Zann, Bentley, & Hau, 2007; Prior, Heimovics, & Soma, 2013).

455 *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
460 et al. 2006). Outdoor and indoor housing environments likely 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 & Gous,
465 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.

470 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
475 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 & Kern, 2014). However, natural weather conditions in the wild are also variable and may have important stimulatory effects.

 Outdoor aviaries may also be subject to varying levels of environmental
480 background noise depending on location, which might affect reproductive success (Halfwerk, Holleman, Lessells, & Slabbekoorn, 2011). 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
485 versus outdoor housing, for the reasons discussed below.

Housing and social effects

The composition and density of breeding groups of zebra finches might affect pair bonding and, in turn, reproductive success. Research in both domesticated (Adkins-
490 Regan & Tomaszycski, 2007; Schweitzer, Schwabl, Baran, & Adkins-Regan, 2014), and wild zebra finches (Mariette & Griffith, 2012b) 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 & Williams, 1998; Holveck & Riebel, 2010). In another estrildid species (the Gouldian finch *Erythrura gouldiae*) females forced paired with incompatible mates had long-term elevated levels of corticosterone (the dominant avian stress hormone; Griffith et al. 2011). Recently, Ihle et al. (2015) found in the zebra finch that freely chosen pairs achieved a 37% higher fitness than experimentally arranged pairs, a finding that is consistent with recent studies in captive bred zoo species that have shown that mating animals to their preferred partner, versus non-preferred or genetically assigned partners, dramatically increased reproductive success (Martin et al. 2012).

In addition to the potential stress caused by force pairing with a non-chosen partner, captive zebra finches also experience stress when separated from their partner during or at the end of experiments (Perez et al., 2012; Ramage-Healey, Adkins-Regan, & Romero, 2003; Schweitzer et al., 2014), although some of this stress might have been due to the stress of social isolation itself. 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
520 close to one another throughout the year (Mariette & Griffith, 2012b) with little evidence of infidelity (Griffith, Holleley, Mariette, Pryke, & Svedin, 2010) or divorce (Zann, 1996), although wild individuals will occasionally 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
525 *Stress physiology*).

The wild zebra finch is a very social bird with groups of individuals often breeding closely together (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 in
530 cages, there is likely to be varying degrees of visual and acoustic communications between individuals in different pairs. There is some evidence from captive birds that reproductive investment is modified by acoustic signals from other members of a loose social group (Waas, Colgan, & Boag, 2005). This is consistent with the finding that in the wild, despite a low level of synchrony across a whole population, pairs
535 nesting very closely to one another synchronise their reproductive activity (Mariette & Griffith, 2012a). However, whilst social contact can have stimulatory effects on some individuals, there may be inhibitory effects on others. In the wild, proximity to others shows great variation with many pairs actively choosing to breed away from colonies in solitary positions (Mariette & Griffith, 2012a). This may reflect an
540 underlying behavioural polymorphism of social and asocial individuals, with the latter perhaps socially inhibited by the close proximity of others (Dall & Griffith, 2014).

Breeding in aviaries 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
545 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, Cathaud, Chambon, & Vignal, 2013; Ruploh, Bischof, & Engelhardt,
550 2012). Reproductive success may be affected by the expression of song in adults, with
key parameters of song structure (complexity, tempo, stereotypy) and output being
affected by the environment (Brumm, Zollinger, & Slater, 2009; Holveck, Vieira de
Castro, Lachlan, ten Cate, & Riebel, 2008) and by the availability of song tutors
during early life (Derégnaucourt, 2011). The early environment also affects the
555 development of song preference behaviour in females (Clayton, 1990b, 1990c;
Riebel, Naguib, & Gil, 2009). There is some evidence of reduced variance in song
structure between wild and domesticated populations (Slater & Clayton, 1991;
Woodgate, Mariette, Bennett, Griffith, & Buchanan, 2012), and it is possible that
there is variation in the quality or variance of song across captive populations.

560 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, Schielzeth, & Forstmeier, 2012; Riebel, 2009;
Woodgate et al., 2012).

565 *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 & Priedkalns, 1985), and indirectly (Williams, 1996a; Williamson et al., 2008) stimulate
570 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
575 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 not to ignore even small changes in humidity, as there
580 remains the possibility that variation in humidity in captive breeding environments can 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 typically humidity is not often controlled to a high level of precision independently of air temperature.

585 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 to breed throughout the winter in temperatures down to as low as 2.2°C (Zann et al., 1995), periods of low temperature are associated with a reduction or cessation of reproductive activity
590 (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, Walzem, & Williams, 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, Sandell, & Nilsson, 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, all of which may lead to different levels of disturbance and stress, which may ultimately result in inadvertent selection on stress-tolerant phenotypes. To date, there have been remarkably few studies investigating these issues in the zebra finch. In their paper, Collins et al. (2008) found that the provision of a food reward (fresh greens) directly after handling helped birds to settle more quickly. 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 timeframe of the experiment (Collins et al., 2008). Whilst Collins et al. (2008) did not look at reproductive performance in the context of these factors, they did find the handling regime (whether they were rewarded after capture) affected attractiveness in mate selection. The recent study by Sorge et al. (2014) demonstrates just how subtle the effects of handling or visiting stress can be on captive animals, with laboratory rodents of several species showing significantly different anxiety and pain responses in the presence of male versus female research technicians.

Diet and nutrition

The basic diet and nutritional supplements provided to breeding zebra finches vary across populations and also across studies within populations and are likely to
620 influence variation in reproductive investment and success (Gorman & Nager, 2003; Patricia Monaghan, Metcalfe, & Houston, 1996; Williams, 1996b). 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 between the quality of seed with some diets
625 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 provided to zebra finches prior and during reproduction can have pervasive effects on reproductive success (and the variation is often intentionally experimental). Female zebra finches
630 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 male zebra finches, diet quality can influence bill and plumage coloration, and
635 courtship rate, all of which can affect female preference and reproductive investment (Atagan & Forst, 2012; Burley, Price, & Zann, 1992; McGraw, Gregory, Parker, & Adkins-Regan, 2003).

In addition to variation in diet quality, laboratories also vary in the manner in which food is provided to breeding zebra finches, which could influence reproductive
640 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
645 food. Access to food could affect reproductive success by influencing individual decisions about mass regulation (Cuthill, Hunt, Cleary, & Clark, 1997), the physiological ability of birds to breed (Rashotte, Sedunova, Johnson, & Pastukhov, 2001; Sandell, Adkins-Regan, & Ketterson, 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).
650

Overall, we need to remain mindful that the zebra finch is highly opportunistic and is likely to adaptively 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
655 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
660 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 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
665 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
670 success.

Stress physiology

Individuals can vary substantially in their endocrine responses to environmental
675 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
680 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 & Williams, 2003), reduced incubation (Edwards,
685 Chin, Burness, Gilchrist, & Schulte-Hostedde, 2013; Spencer, Heidinger, D'Alba, Evans, & Monaghan, 2010; Thierry, Massemin, Handrich, & Raclot, 2013), lower nestling provisioning (Almasi, Roulin, Jenni-Eiermann, & Jenni, 2008), greater nest abandonment (Spée et al., 2011; Strasser & Heath, 2013), and lower reproductive success (fewer offspring fledged; Schmid et al. 2013). In captive zebra finches,
690 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, 695 Buchanan, & Goldsmith, 2006; Spencer, Evans, & Monaghan, 2009), and perhaps most surprisingly 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 selected for over time, resulting in captive populations with dampened stress responses. Anecdotally, it is apparent that 700 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 705 stress responses compared to domesticated congeners (Homberger, Jenni-Eiermann, Roulin, & Jenni, 2013; Suzuki, Yamada, Kobayashi, & Okanoya, 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.

710 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; Ramage- 715 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 (Scarлата et al., 2012; Shepherdson, Carlstead, & Wielebnowski, 2004), the effect of anthropogenic disturbance on reproductive success in free-living birds (Crino, Johnson, Blickley, Patricelli, & Breuner, 2013; Crino, Van Oorschot, Johnson, Malisch, & Breuner, 2011; Müllner, Eduard Linsenmair, & Wikelski, 2004; Walker, Boersma, & Wingfield, 2005), and the general welfare of captive animals (Fanson, Lynch, Vogelnest, Miller, & Keeley, 2013; Lane, 2006; Whitham & 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.

730

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 variation – and what selection pressures might maintain this variation (Wolf & Weissing, 2012). There is as yet little information on wild zebra finches, but domesticated zebra finches, like wild birds of other species, show variation across personality traits such as boldness, exploratory behaviour, activity, neophobia, and aggressiveness (Beauchamp, 2000; Brust, Wuerz, & Krüger, 2013; David & Cézilly, 2011; Martins, Roberts, Giblin, Huxham, & Evans, 2007; Schuett, Godin, & Dall, 2011), raising questions as to how this might directly or indirectly affect mate choice, fertilization

740

success, and/or parental care, and whether sexual selection contributes to maintaining inter-individual variation in personality traits (Schuett, Tregenza, & Dall, 2010).

In breeding zebra finches, personality may influence the speed and willingness with which an individual chooses a mate (David & Cézilly, 2011). Variation in female choosiness may be particularly relevant to variation in reproductive success when 745 males and females are force paired in cages; very choosy females may simply abstain from copulating with the male she is provided. 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, 750 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). Future work comparing captive raised and cross-fostered individuals from several wild and domesticated populations should help to test whether variation in 755 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). 760 Both mate preference tests (Schuett, Godin, et al., 2011) 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 765 reproductive success (Royle, Schuett, & Dall, 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 generates personality variation that affects reproductive success. Unintentional selection for certain personality traits may result from biases in the 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 & Foster, 2006; Riebel et al., 2009) and also the specific choice of partner, with individuals pairing assortatively for quality (Holveck & Riebel, 2010). Recent work in the zebra finch has demonstrated striking relationships between the extent of loss of telomere length during early development and longevity (Heidinger

790 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
795 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, Segelbacher,
Mueller, & Kempenaers, 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
800 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
805 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
810 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 & Frankham, 2003; Heath, Heath,
Bryden, Johnson, & Fox, 2003), or through genetic drift (Woodworth, Montgomery,
Briscoe, & Frankham, 2002). Two studies have found morphological differences

815 between wild and domesticated birds, and between different subsets of the
domesticated population (Carr & Zann, 1986; Forstmeier et al., 2007). Reassuringly,
despite this morphological divergence between populations, Tschirren et al. (2009)
found that life-history trade-offs between traits were very similar between wild and
domestic birds held in captivity. Even without intentional selection, the data we
820 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
825 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.
830 (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).

835 Although many studies 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) has been found to correlate with various life history traits (Meunier,
Figueiredo Pinto, Burri, & Roulin, 2011), through trade-offs associated with the

840 melanocortin system itself (Ducrest, Keller, & Roulin, 2008), and as a component
of behavioural syndromes (Emaresi et al., 2014; McKinnon & Pierotti, 2010). In zebra
finches, relatively few studies have specifically examined the effects of colour
variants on behaviour or physiology, finding effects on sexual imprinting and song
learning behaviour (Mann, Slater, Eales, & Richards, 1991; Vos, Prijs, & Tencate,
845 1993), and the visual system (Bredenkötter & Bischof, 2003; Eckmeier & Bischof,
2008).

Second, a recent molecular analysis found that white morphs represented a
distinct genetic cluster, reflecting their history of selective breeding (Hoffman,
Krause, Lehmann, & Krüger, 2014). In the process of selecting for these colour
850 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,
855 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
860 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.

865 Accurate genetic pedigrees are likely 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
completely evaluate the extent to which inbreeding effects might contribute to
variation in reproductive success amongst different populations or laboratories.
However, using the zebra finch as a model a recent study has demonstrated a new
870 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 (Forstmeier et al 2012).
875 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
880 inbreeding (Armbruster & 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
885 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, Edwards, &
890 Clayton, 2010; Larson & 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
895 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.

900

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,
905 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
910 likely to be variation in the housing and husbandry practices of different laboratories.
Research groups are often faced with constraints, and have to make strategic decisions
on the basis of space or monetary considerations as well as following different
opportunities to optimise local welfare considerations. Although more standardised

conditions across laboratories might be the most desired outcome, at the least we
915 suggest that further consideration should be given to the way heterogeneity in
conditions and protocols across different studies may affect outcomes and 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
920 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
925 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.

930 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 supporting future empirical zebra finch work will facilitate later attempts
to review and analyse variation across studies.

935

Recommendation

We propose that all future work on captive zebra finches includes the information
itemised in Table 4. We suggest that this data could be presented in a Table provided

either in the Methods section or as Supplementary material. The information
940 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
945 harvest and utilise the material presented.

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Figure Legends

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Figure 1. In this illustrative example (not real data) the frequency distribution is illustrated showing 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.

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Figure 2. Mean number (\pm 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 of these females were successful but there are significant differences in how many fledglings they produced when they fledged offspring (see results). All data were from the longitudinal study by Varian-Ramos et al (2014).

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Figure 3. The proportion of females (\pm s.e.) that successfully fledge offspring when given the opportunity to breed, across different institutions.

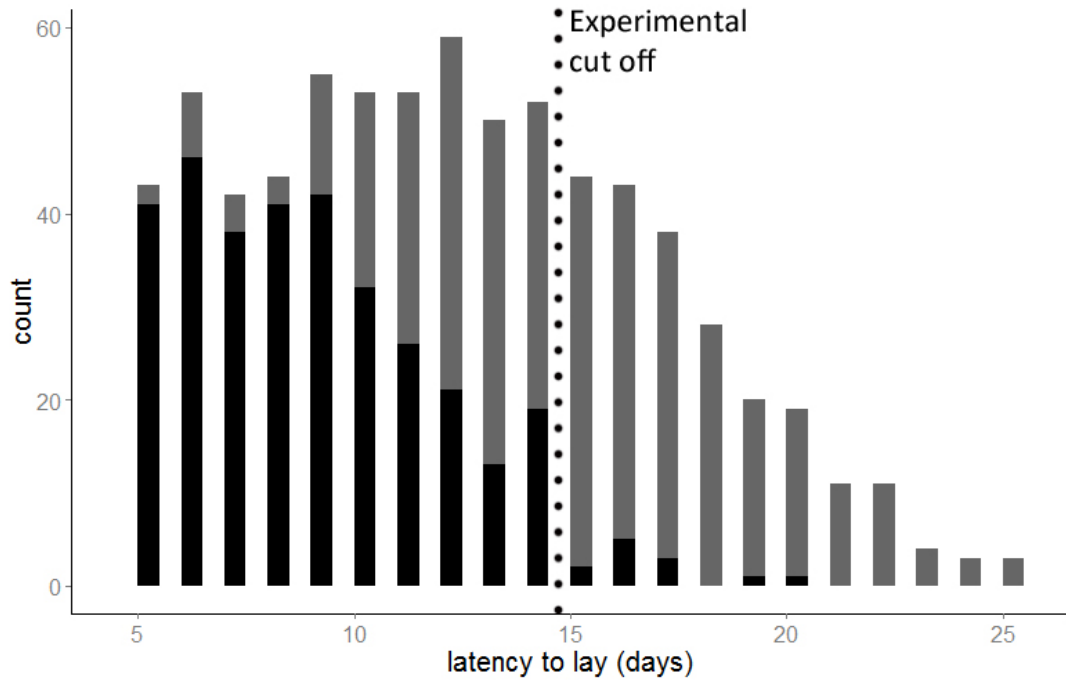
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Figure 4. The reproductive output of females when given the opportunity to breed measured through two metrics; producing a clutch (a & b), and producing fledglings (c & d). Females were examined across two categories: either force-paired or free-choice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

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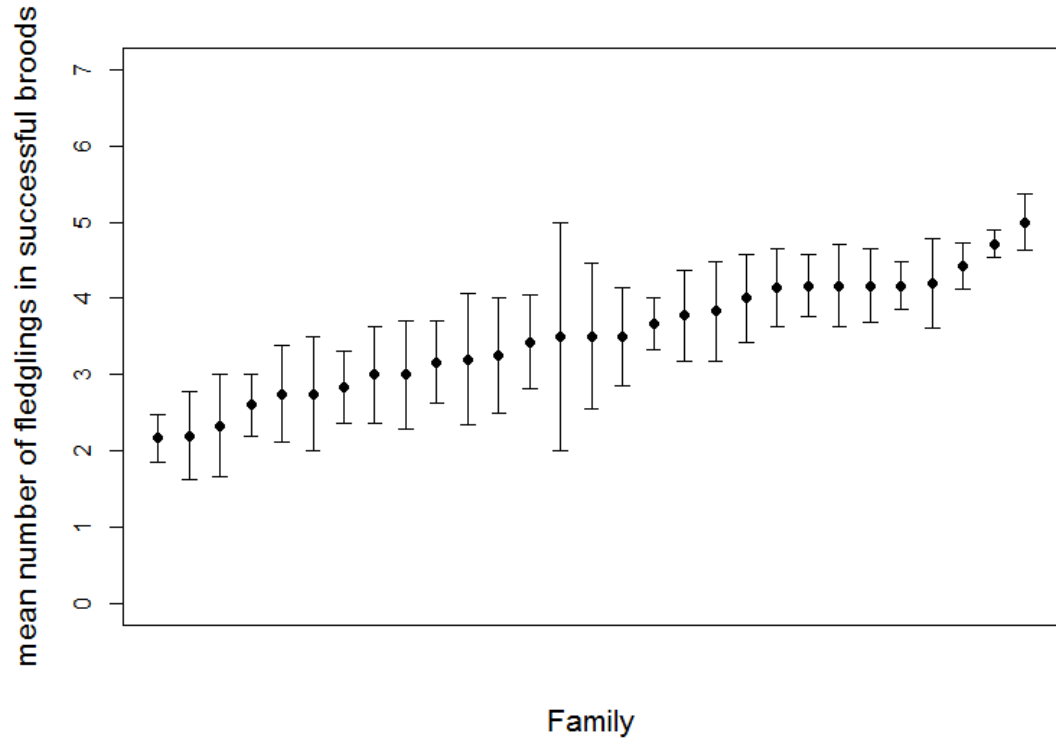
Figure 1

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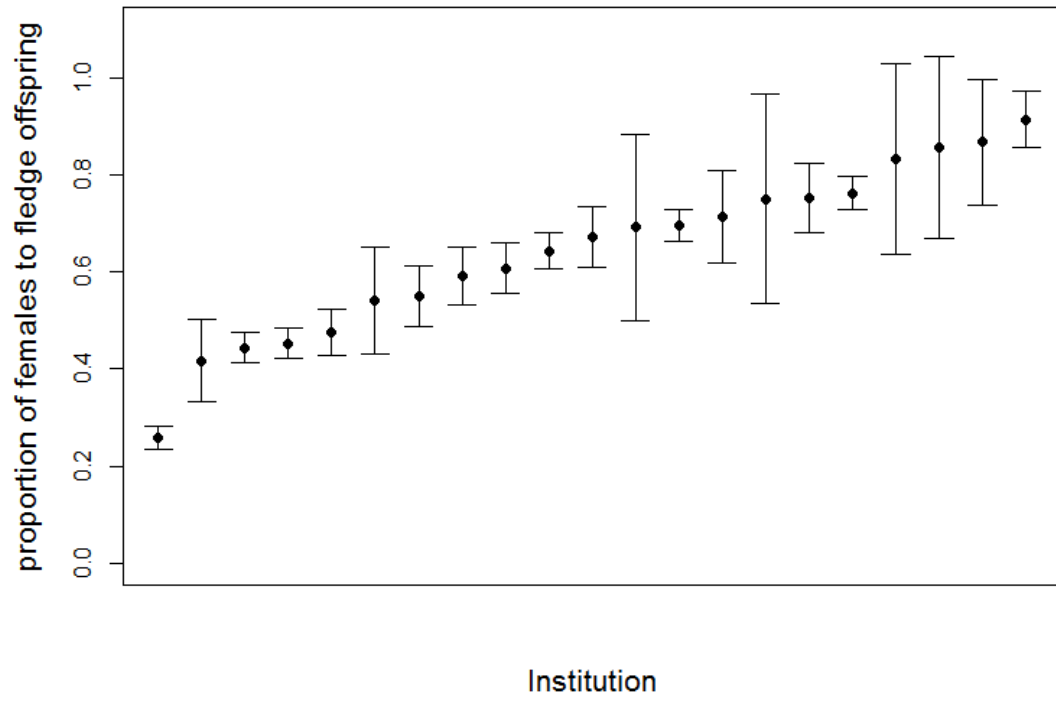
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Figure 2.



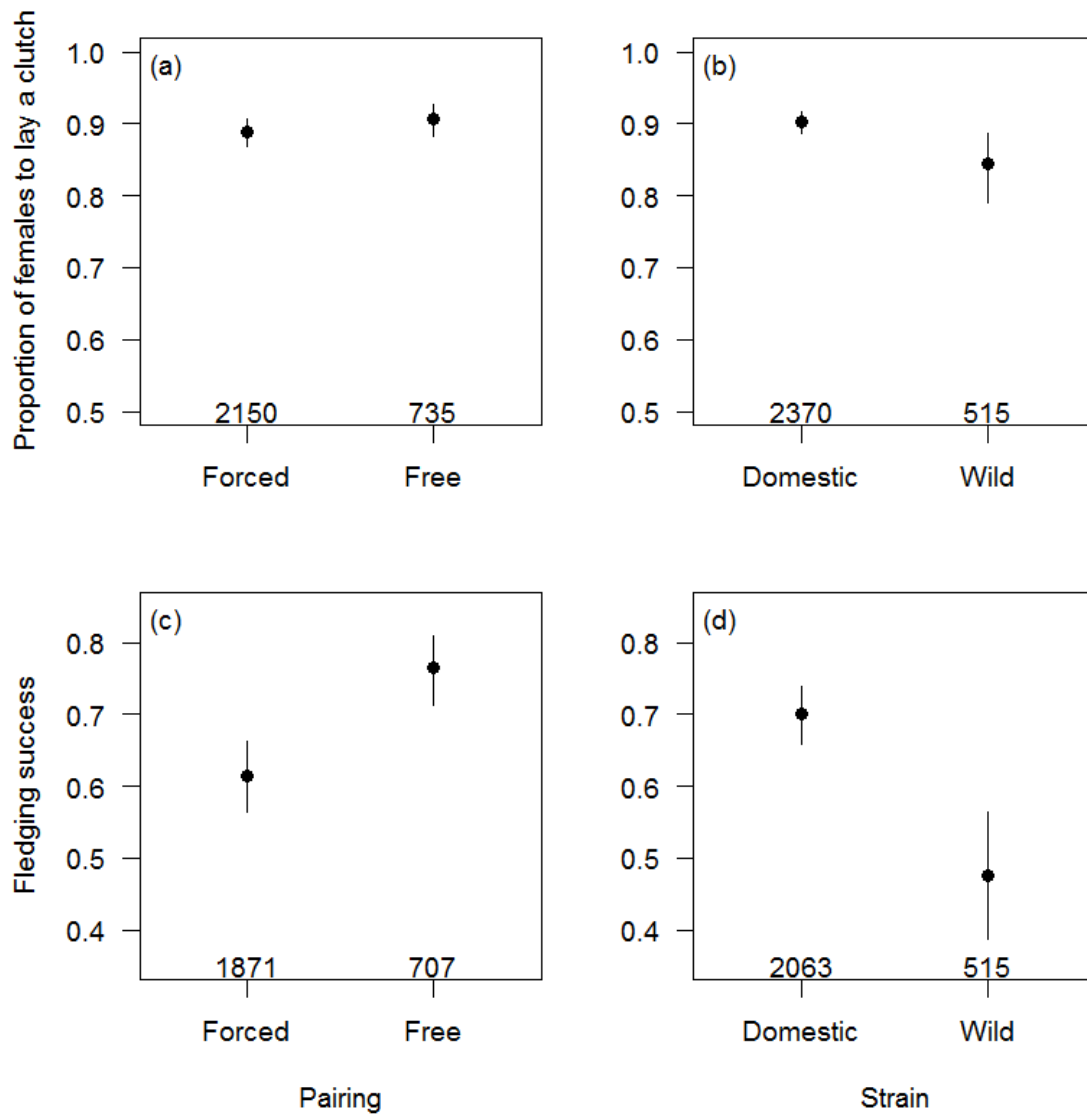
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1550 Figure 3.



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Figure 4.



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