

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

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Abstract

Our understanding of fundamental organismal biology has been disproportionately
65 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
70 (*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
75 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
80 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
85 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

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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,

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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

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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

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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.

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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).

115 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.
120 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
125 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
130 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.,
135 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
140 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
145 (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
150 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
155 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
160 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
165 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
170 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.

175 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
180 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
185 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
190 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
195 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
200 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
205 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
210 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
215 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
220 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
225 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
230 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
235 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

240 **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
245 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
250 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
255 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-
260 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
265 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).
270 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
275 failure may be attributable to individual differences.

Statistical methods

Our statistical analyses were focused on addressing individual repeatability of
280 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
285 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

290 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
295 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
300 (<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
305 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
310 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).

315 **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
320 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
325 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, $P < 0.001$).

330 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
335 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, $\text{Pr}(\text{difference} < 0) = 0.45$).

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
 345 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 ($\chi^2 = 378.05$, $df = 69$, $P < 0.001$, $n = 3213$) and institutions ($\chi^2 = 122.37$, $df = 22$, $P < 0.01$). Similarly, the probability of producing fledglings was different across studies ($\chi^2 = 575.15$, $df = 56$, $P < 0.001$, $n = 2906$, Figure 3) and across institutions ($\chi^2 = 311.45$, $df = 20$, $P < 0.001$).
 350 = 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; $\Pr(\text{difference} < 0) = 0.025$, $n = 3213$ 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
 355 of grouping (study: ICC = 0.27, s.e. = 0.043; institution: ICC = 0.19, s.e. = 0.061; $\Pr(\text{difference} < 0) = 0.15$, $n = 2906$).

Reproduction and pair and female characteristics

Females were as likely to produce a clutch when housed either indoors or outdoors
 360 (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

365 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
370 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
375 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
380 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

385 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

390 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
395 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
400 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
405 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
410 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).

415 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
420 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
425 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 430 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
435 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

440 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
445 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
450 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.
455 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
460 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
465 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,
470 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
475 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
480 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
485 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).

490 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
495 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

500 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
505 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
510 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; 515 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 520 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 525 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 530 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 535 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.

540 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
545 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
550 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).
555 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
560 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.

580 *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
590 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
595 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.

600 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).
605 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
610 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

640 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).

655 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).

665 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
670 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
675 (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
680 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.

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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. 690 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 695 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 700 (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 705 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, 710 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
715 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 (Hombberger et al., 2013; Suzuki et al., 2012). Corticosterone has broad pleiotropic effects on physiology and behaviour (Sapolsky, 2000).
720 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
725 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-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
730 housing conditions and the efficacy of breeding programs in zoo animals (Scarлата 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
735 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.

740

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
745 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
750 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
755 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
760 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 cross-

fostered individuals from several wild and domesticated populations should help to test whether variation in choosiness is more pronounced on the population or
765 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
770 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
775 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.

780 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
785 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.

790 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
795 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.

800 **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
805 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
810 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
815 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
820 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
825 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
830 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
835 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.,

840 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),

845 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),

850 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

855 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

860 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
865 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
870 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
875 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
880 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.,
885 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.

890 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
895 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; Eklom & Galindo 2011), and transcriptome sequencing (e.g. Mortazavi et al. 2008; Wang et al. 2009; Eklom et al. 2014), which will help in the identification of
900 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
905 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.

910 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

915 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

920 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).

925 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

930 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

935 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
940 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
945 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
950 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
1465 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.

1470

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 29 females were successful but there are significant differences in how many
1475 fledglings they produced (see results). All data were from the longitudinal study by Varian-Ramos et al. (2014).

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

1480

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 Cínicos, 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 Cínicos, 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 Cínicos, 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 Cínicos, 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 ^h	5	12	-	-	92	-	AN, MT
Lund University, Sweden ^h (Naïve)	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 (Naïve)	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 ⁱ	26	4 weeks to lay	25	17	3.76 ± 1.44	96	65	DLH, RN	
University of Glasgow, UK (2007, Naïve)	D	I	Forced ⁱ	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, PV
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, PV
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 ⁱ	11	10	11	8	4.00 ± 1.58	100	73	MJH, KR
University of Leiden, Netherlands - 2006	D	I	Forced ⁱ	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	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

- 1490 ^aThe number of females that were given the opportunity to breed including those that died during the experiment
^bThe 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
^cThis 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)
^cThe percentage out of all females given the opportunity
- 1495 ^gAll females produced at least one clutch, but 9 out of the 45 females (20%) produced clutches in which all eggs were infertile
^hTime 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.
- 1500 ⁱFemales (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.
^jBirds first participated in mate preference test, then one male + one female of preferred or non-preferred category were paired
^kThe 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
 1505 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

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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 x 100	6-8	14L:10D	22	30-70%	Chopped up hard boiled egg with shells on Greens, egg	Schweitzer et al., (2014)
Univ. Glasgow, UK	Cage	60 x 45 x 40	1	16L:8D	22		Egg and vitamins	Gorman and Nager (2003)
Lancaster Univ., UK	Cage	120 x 45 x 40	1	16L:8D	20		Egg food (Witte Molen, the Netherlands), greens	Mainwaring et al., (2012)
Lund Univ., Sweden	Cage	32 x 48 x 32	1	14L:10D	18-24			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 x 40 x 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 x 40 x 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 x 30 x 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)

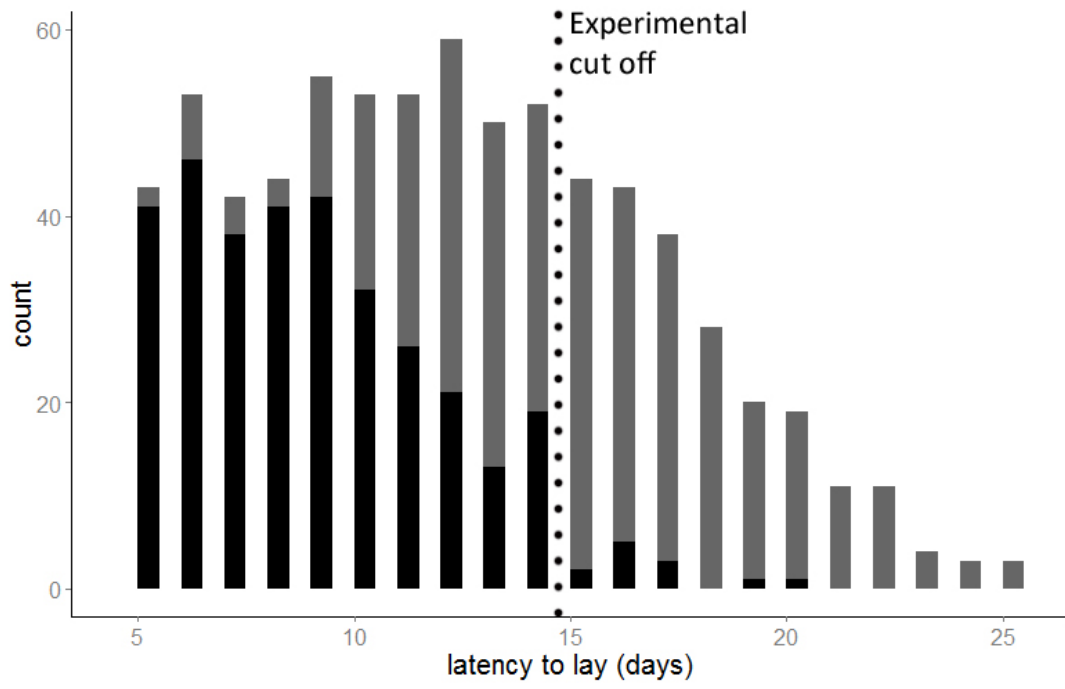
Table 4. A proposed set of data to be completed in all future publications reporting on work focused on the zebra finch.

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Aspect	Item	Detail
Study Design	N experimental groups	
	N control groups	
Numbers used	Nature of replication	e.g. whole experiment was conducted twice
	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	
Experimental Procedures	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
	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
Housing and husbandry	Any bias in selection of individuals	e.g. only birds with breeding experience used
	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
Average number of fledglings		mean ± standard deviation (excluding zeros)

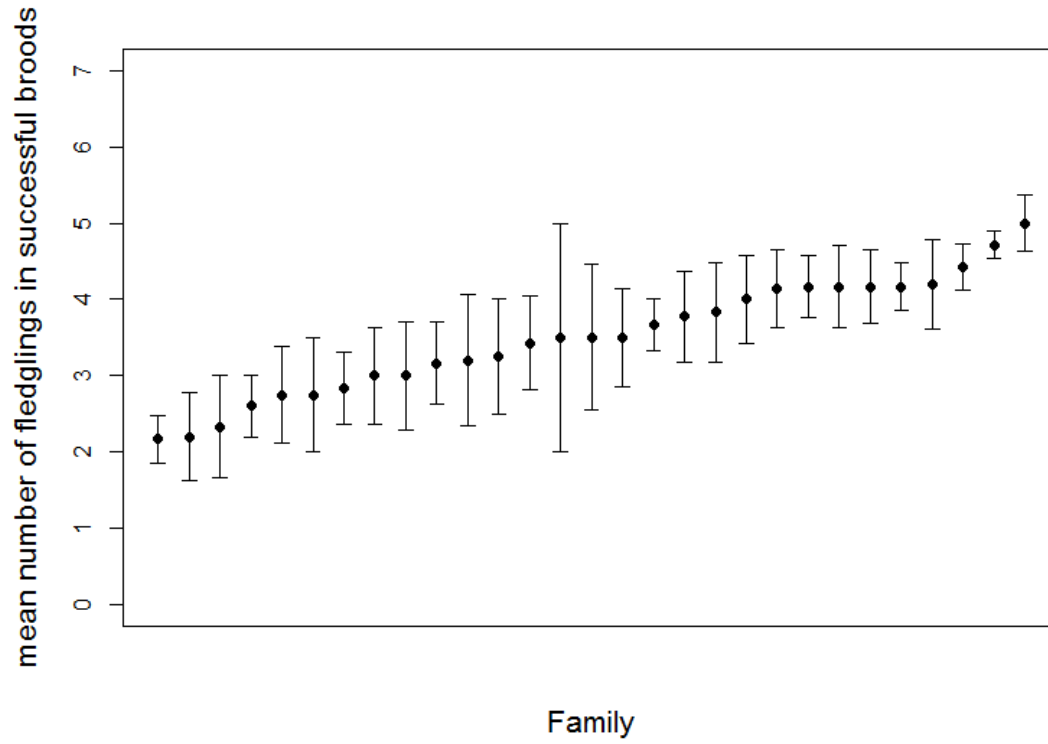
Figure 1

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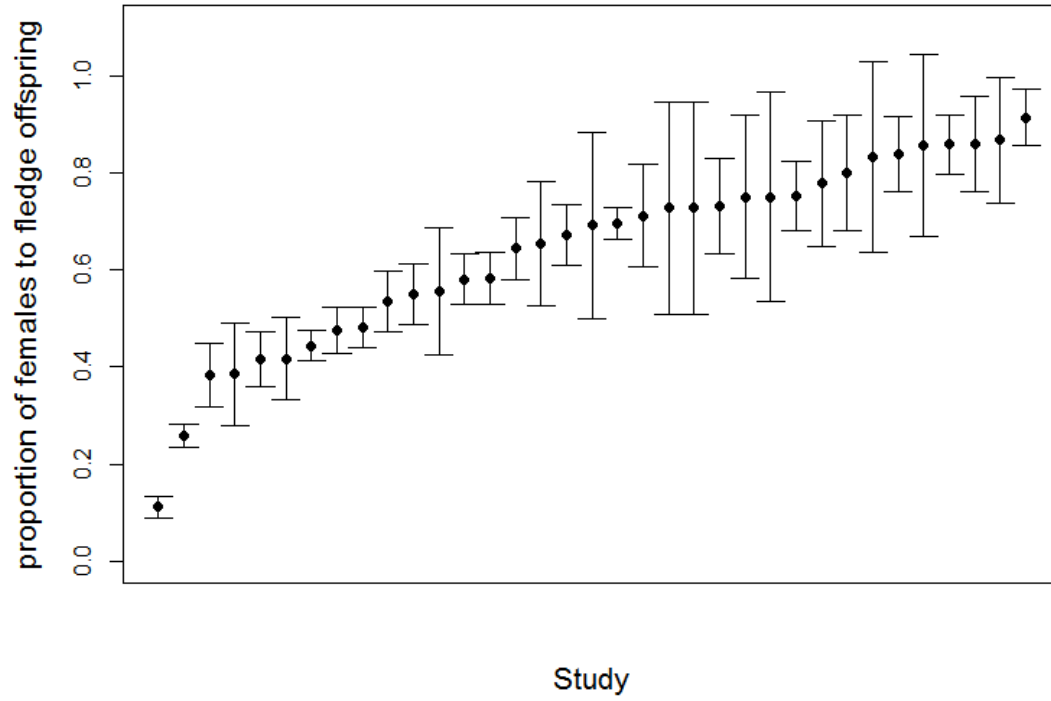
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Figure 2.



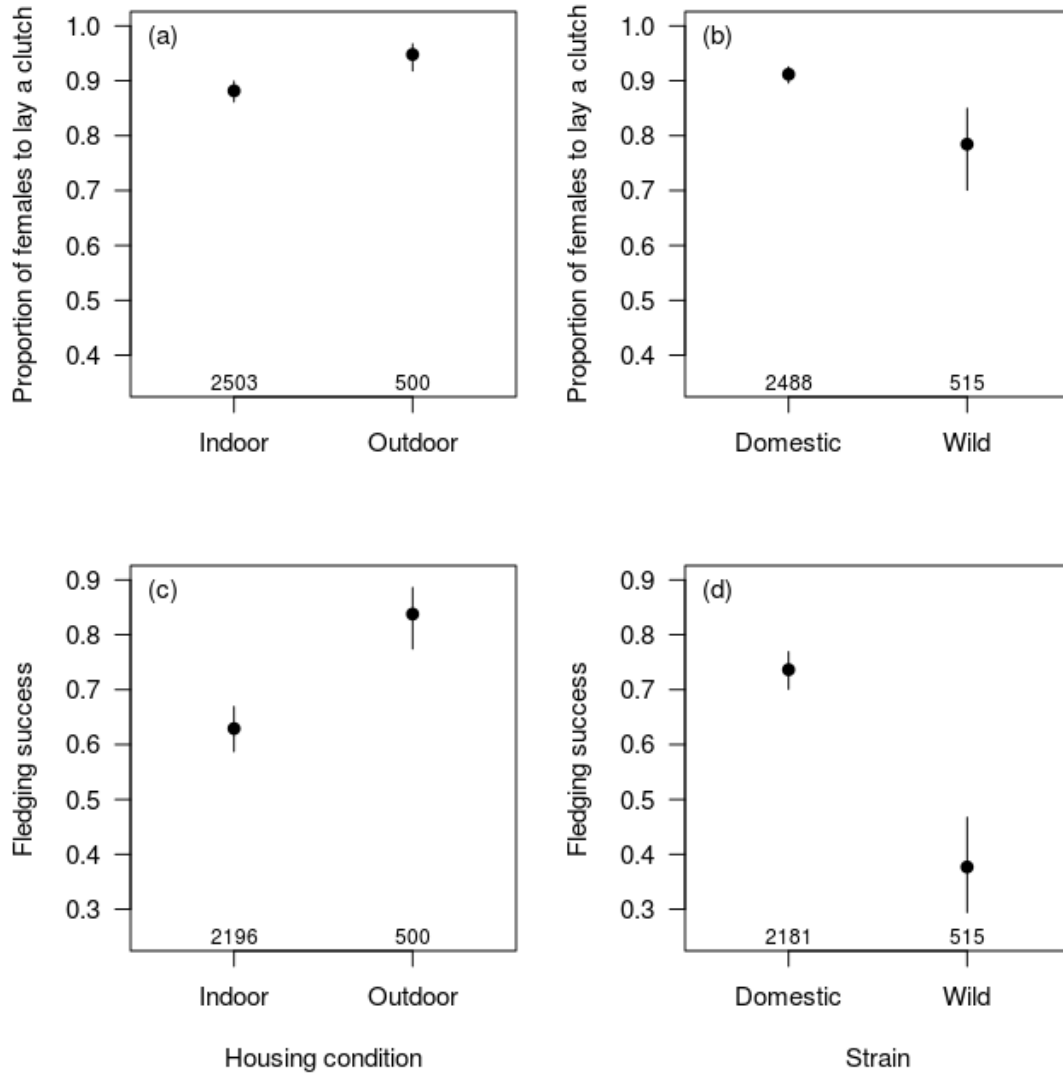
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1540 Figure 3.



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Figure 4.



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