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Variation in Reproductive Success Across Captive Populations: Methodological Differences, Potential Biases and Opportunities

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PERSPECTIVES AND REVIEWS

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 influenced by studies of a relatively small number of ‘model’ species extensively studied in captivity. Laboratory populations of model

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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*). This important model species is used for research across a broad range of fields, partly due to the ease with which it can be bred in captivity. However despite this perceived amenability, we demonstrate extensive variation in the success with which different laboratories and studies bred their subjects, and overall only 64% of all females that were given the opportunity, bred successfully in the laboratory. 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 research outcomes across studies. The zebra finch remains an excellent captive animal system and our aim 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. We hope to improve systematic reporting methods and that further investigation of the issues we raise will lead both to advances in our fundamental understanding of avian reproduction as well as to improvements in future welfare and experimental efficiency.

Introduction

There has been a recent call to improve on the reporting of information supporting empirical work conducted on animals to improve evaluation and interpretation, and facilitate the use of data in further work (Kilkenny et al. 2010). In their paper, Kilkenny et al. (2010) outlined the value of capturing contextual information (e.g. animal backgrounds, housing and husbandry conditions, sample sizes and selection procedures) with a set of guidelines identifying 20 items that should be addressed in each publication. One of the main underlying drivers of this effort was to reduce the amount of clinical research using laboratory animals (through the UK-based National Centre for the Replacement, Refinement and Reduction of Animals in Research). However, in their paper Kilkenny et al. (2010) also highlighted the opportunities that are missed when the context of a particular study is not adequately communicated. While they focused on all animal models, and particularly those used in biomedical research, there were also some clear messages for research in animal behaviour. The issues raised by Kilkenny et al. (2010), and related ones outlined below will result in biases in both experimental selection of subjects and evolutionary selection over both long and short timescales. 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. Ultimately we hope our work raises an awareness of the effects that the experimental context may have on research outcomes. The issues on which we focus 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 programmes for the benefit of animal conservation (Lees & Wilcken 2009).

In two well-monitored populations of zebra finches 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 (Zann et al. 1995; Griffith et al. 2008). Even when predation was reduced through the provision of nest boxes, only 53% of clutches resulted in fledged offspring (Griffith et al. 2008). The variation in reproductive success in the wild is an interesting question in evolutionary ecology that must ultimately reflect the individual optimization 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, many individuals fail to reproduce. Zebra finches are not the exception to the rule, as individuals in many animals species brought into captive breeding programmes from wild populations fail to reproduce to recruitment (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 captive breeding is becoming an increasingly important tool to guard against extinction in conservation and species management programmes. Thus, careful evaluation of reproductive failure seen in extensive, multi-institutional captive breeding programmes, such as the zebra finch, and other model systems, can provide valuable insight for the planning and design of conservation-focused captive breeding programmes (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 (Zann 1996; Griffith & Buchanan 2010). It is important to understand how reproductive failure in laboratory populations might affect the ability to replicate studies across laboratories and indeed affect research outcomes themselves. Not all individuals respond similarly when given the opportunity and resources to reproduce: some individuals quickly and repeatedly reproduce regardless of the circumstances, while others fail to reproduce at all over a lifetime in captivity. The variance in reproductive success among individuals within a single population has been the explicit target of some studies (e.g. Alonso-Alvarez et al. 2006; Bolund et al. 2009; McCowan et al. 2014). However, more generally it is ignored in papers, and in practice could lead to the 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 made to additional birds that were given the opportunity but did not lay eggs (e.g. in Gorman et al. 2005, 77% of females produced a clutch). Even among those individuals that initiate a reproductive attempt, there is variation in their ability to hatch eggs and rear offspring through to independence. Only rarely is this variation specifically the focus of analysis or comment, even in papers that are focused on aspects of reproductive behaviour or physiology. The variation in these aspects of individual reproductive success in domesticated populations will affect the number of offspring that an individual leaves in subsequent generations. As a result, the underlying determinants of this variation are subject to sexual, natural and artificial selection. The variation among individuals in reproductive success in captive populations will include biological traits such as individual behavioural, genetic and physiological differences, and those relating to the physical, nutritional and social environment in which individuals are held. Here, we introduce each key parameter in the context of the zebra finch, before characterizing the variation that exists across laboratory populations in reproductive success.

Part I. Biological Determinants of Variation in Reproductive Success in Captivity

Genetic background

Zebra finches were first exported to Europe from Australia in the 1870s 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 (Zann 1996; Forstmeier et al. 2007) where they have subsequently been isolated to an unknown and varying degree at local and national levels. Domesticated zebra finches used in research in Europe and North America are mostly derived from populations maintained by amateur and professional finch breeders who have bred these populations for over a hundred years without an influx of wild-caught birds from Australia (Zann 1996). Typically, captive zebra finches have not been bred with the intention of preserving genetic diversity and natural behaviour, because these are not priorities for the amateur and professional aviculturists who maintain most of the zebra finches in the overall captive population (even though some laboratories may manage their stock to optimize these). Finch breeders are partly driven by the creation of new morphs that are selected by line breeding and backcrossing, to the extent that there are now 30 recognized colour variants, from a single wild-type phenotype (Zann 1996). Even 'wild-type' birds are bred for competitive showing and judged against aesthetics and avicultural standards such as large size. As a result of this history, domestic populations may have diverged genetically from their wild conspecifics, through artificial selection imposed by aviculture, natural selection to captive conditions (Gilligan & Frankham 2003; Heath et al. 2003), or through genetic drift (Woodworth et al. 2002). Two studies have found morphological differences between wild and domesticated birds, and between different subsets of the domesticated population (Carr & Zann 1986; Forstmeier et al. 2007).

Reassuringly, despite this morphological divergence between populations, however, life-history trade-offs between traits appear very similar between wild and domestic birds held in captivity (Tschirren et al. 2009).

To date, just a single study has addressed genetic divergence in the domesticated zebra finch. Forstmeier et al. (2007) used microsatellites to analyse 18 captive research populations and two wild populations. 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). While it does support the idea of fragmentation of the domestic population, the limited neutral genetic divergence between populations observed by Forstmeier et al. (2007) does not exclude a higher degree of divergence in functional traits across these domestic populations.

Although many researchers work with ‘wild-type’ birds, the presence of the colour variants in the background population, or directly in some studies, raises some issues. First, the degree of melanin pigmentation in animals (a likely target of much artificial selection) correlates with various life-history traits (Meunier et al. 2011), through trade-offs associated with the melanocortin system itself (Ducrest et al. 2008), and as a component of behavioural syndromes (McKinnon & Pierotti 2010; Emaresi et al. 2014). Relatively few studies have specifically examined the effects of colour variants on zebra finch behaviour or physiology. Two studies found effects on sexual imprinting and song learning behaviour (Mann et al. 1991; Vos et al. 1993). Two studies found effects on the visual system (Bredenkötter & Bischof 2003; Eckmeier & Bischof 2008). Nevertheless, a recent molecular analysis found that white morphs represented a distinct genetic cluster, reflecting their history of selective breeding (Hoffman et al. 2014). In the process of selecting for these colour variants, there may have been unintentional side effects on other traits, through genetic hitchhiking, selective sweeps or epistasis. While there have been no investigations of this in the zebra finch, there are examples in other domesticated systems (e.g. rats: Will et al. 2003; Overstreet et al. 2005; dogs: Sutter et al. 2004). The effects of such genetic correlations in the zebra finch might be particularly likely, given that the genome of the domesticated zebra finch consists of few, relatively large linkage blocks compared with other vertebrate genomes (Backström et al. 2010).

As well as potential divergence between different domesticated populations, most studied birds are part of small isolated populations, vulnerable to inbreeding. Studies of one of the larger research populations have demonstrated that experimental full-sibling pairings suffering reduced reproductive success (Bolund et al. 2010). Individuals actively avoid mating with familiar siblings (Ihle & Forstmeier 2013), and a recent study of another captive population revealed a sensitivity to olfactory cues of kinship, with females reducing reproductive investment when paired with close relatives (Caspers et al. 2015). As stressful environments can exacerbate the effects of inbreeding (Armbruster & Reed 2005), housing and other stressors that differ across laboratories might drive variation in the effect of inbreeding depression across different studies, as well as the frequency of deleterious alleles will vary due to population history. Therefore, the further consideration of the genetic background and stochastic differences between different study populations may help to explain some differences in the research outcomes across studies, and these might be better resolved with new genomic approaches (e.g. Mortazavi et al. 2008; Wang et al. 2009; Metzker 2010; Davey et al. 2011; Ekblom & Galindo 2011; Ekblom et al. 2014).

Individual differences

Domesticated zebra finches vary across personality traits such as boldness, exploratory behaviour, activity, neophobia and aggressiveness (Beauchamp 2000; Martins et al. 2007; David & Cézilly 2011; Schuett et al. 2011b; Brust et al. 2013), raising questions as to how this might directly or indirectly affect components that determine reproductive success (Schuett et al. 2010).

Personality may influence the speed and willingness with which an individual chooses a mate (David & Cézilly 2011), and very choosy individuals may simply refrain from pairing with the bird they are allocated, if they are not behaviourally compatible. Over time, this could result in inadvertent selection for less choosy birds in captive-bred populations. A recent study of wild and domesticated populations of the house mouse *Mus musculus* (Slade et al. 2014) demonstrated significant changes in mate preference behaviour within a few generations.

In species such as the zebra finch with biparental care, mate choice based on assortative mating for personality could moderate sexual conflict in parental care, altering reproductive success (Royle et al. 2010). Pairs with similar personalities may reproduce more successfully because that may allow for greater coordination of reproductive and parental behaviours

(Schuett et al. 2011a; Mariette & Griffith 2012a; Both et al. 2005; but see Schielzeth et al. 2010; McCowan et al. 2014).

There is preliminary evidence that some individuals cope better with particular captive conditions (Crino et al. 2016), and some personality types have greater reproductive success in captivity (McCowan et al. 2014). 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 (Immelmann 1972; Clayton 1990b,c) to an extent that subspecies-specific preferences can be easily reversed (reviewed in Clayton 1990a). Phenotypic quality and individual condition can influence both female mate selectivity (Burley & Foster 2006; Riebel et al. 2009) and phenotypic preferences (Holveck & Riebel 2010). Furthermore, recent work has demonstrated that 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 the pattern of an individual's reproductive investment strategy throughout life.

Stress physiology

Individuals can vary substantially in their endocrine responses to environmental stimuli that can, in turn, cause dramatic variation in reproductive behaviours (e.g. Lendvai & Chastel 2010). For example, in captive zebra finches, some individuals might be more susceptible to stressors associated with housing conditions such as cage conditions, population density and exposure to caregivers. In birds, stressors activate the hypothalamic–pituitary–adrenal (HPA) axis and result in the release of the steroid hormone corticosterone (reviewed in Cockrem 2013). Corticosterone elicits physiological and behavioural responses that help birds prioritize self-maintenance and survival at the expense of reproduction (reviewed in Wingfield & Sapolsky 2003). Across bird species, corticosterone is associated with delayed clutch initiation (Salvante & Williams 2003; Griffith et al. 2011), reduced incubation (Spencer et al. 2010; Edwards et al. 2013; Thierry et al. 2013), lower nestling provisioning (Almasi et al. 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, 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 (Evans et al. 2006; Spencer et al. 2009; Adkins-Regan et al. 2013), and even by the stress profile of their partners (Monaghan et al. 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 (S. C. Griffith and W. Forstmeier pers. obs.). Although not yet systematically explored in zebra finches, physiologically dampened stress responses have been documented in grey partridges (*Perdix perdix*) and white-backed munia (*Lonchura striata*) with wild-derived birds having higher stress responses compared with domesticated congeners (Suzuki et al. 2012; Homberger et al. 2013). Corticosterone has broad pleiotropic effects on physiology and behaviour (Sapolsky 2000). Inadvertent selection for individuals with low stress responses is likely to have organismal consequences beyond modifications in stress physiology.

Individual- and population-level HPA axis characteristics may provide a useful way of comparatively testing the deleterious physiological effects of potential sources of reproductive failure as reviewed herein. For example, studies using direct measures of corticosterone can evaluate the relative stress of widespread practices such as forced-pairing (Griffith et al. 2011), mate separation (Remage-Healey et al. 2003; Perez et al. 2012), food restriction (Spencer et al. 2005) and housing conditions such as artificial lighting (Maddocks et al. 2001; Evans et al. 2012). HPA axis characteristics have been used as a tool to diagnose the stressfulness of housing conditions and the efficacy of breeding programmes in zoo animals (Shepherdson et al. 2004; Scarlata et al. 2012), the effect of anthropogenic disturbance on reproductive success in free-living birds (Müllner et al. 2004; Walker et al. 2005; Crino et al. 2011, 2013) and the general welfare of captive animals (Lane 2006; Fanson et al. 2013; 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, that is reducing the strength of selection for 'stressor-resistant" phenotypes, and the biases that it introduces.

Part II. Environmental Determinants of Variation in Reproductive Success

Most research laboratories keep birds in controlled rooms to remove the confounding effects of temperature, light and humidity variation on experimental work, but set points do vary for these parameters (see Table 1). Other sources of variation between research laboratories will also include differences in housing conditions and basic husbandry practices. In the wild, zebra finches are opportunistic breeders that use a range of environmental cues to optimize reproductive success (Zann 1996). In contrast to the generally predictable and primarily photoperiod-dependent development of reproductive systems typical of seasonally breeding passerines (reviewed in Dawson et al. 2001; Sharp 2005), the physiological reproductive axis of zebra finches can respond rapidly to favourable breeding conditions, seemingly at any time of year, despite showing some seasonality to their reproduction (Perfito et al. 2006; Williamson et al. 2008; Zann 1996; reviewed in Hahn et al. 2008). However, individual pairs vary in the timing of breeding in response to these environmental cues, leading to a relatively low level of breeding synchrony within a local population (Zann et al. 1995; Griffith et al. 2008; Mariette & Griffith 2012a). This reproductive plasticity means that for domesticated zebra finches even slight variation in housing conditions (e.g. light regime, humidity, food quality, housing density) may have significant repercussions on breeding success. For example, although photo-stimulation appears to affect testes size (Bentley et al. 2000), it is thought that this effect is due to the extended feeding times available at longer daylengths (Perfito et al. 2008). Both field and laboratory studies indicate that individuals are not constantly in a state of breeding readiness, but rather they cycle through breeding and non-breeding periods, which correspond to distinct neuroendocrine states (Perfito et al. 2007; Prior et al. 2013). Even under constant environmental conditions, it may be the case that individual zebra finches will regulate their breeding activity and go through periods of breeding rest and may not be physiologically ready to breed when an experiment is started.

Indoor vs. outdoor housing

Across studies, there is extensive variation in the basic housing conditions in which breeding birds are kept (see Table 1). 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 will 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 synthesize vitamin D resulting in better growth and egg production (Lewis & Gous 2009). The natural lighting of outdoor housing can also be less stressful for breeding birds compared with the artificial lighting of indoor housing that can cause an increase in glucocorticoid stress hormones (see *Stress Physiology*; Evans et al. 2012). Artificial lighting may also vary qualitatively across research laboratories depending on the total luminance and whether full daylight spectrum lights are used.

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

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

Table 1: The variation in the housing, density, and dietary supplements in some recent studies of captive zebra finch

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

Housing and the social environment

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 & Tomaszycki 2007; Schweitzer et al. 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 2 and references therein). In the zebra finch, females force-paired to males that are preferred in prior mate choice trials, laid slightly more eggs or laid the first egg of their clutch sooner, compared with females paired with non-preferred males (Balzer & Williams 1998; Holveck & Riebel 2010). In their recent study, Ihle et al. (2015) found that individuals that were allowed to freely chose a partner achieved a 37% higher fitness than did experimentally force-paired birds. That finding is consistent with recent studies in a number of captive-bred zoo species in which animals mated to their preferred partner, rather than to non-preferred or breeding-programme assigned partners (often for genetic management), experienced dramatically increased reproductive success (Martin & Shepherdson 2012).

In addition to the potential stress caused by forced-pairing, captive zebra finches also experience stress when separated from their partner during or at the end of experiments (Remage-Healey et al. 2003; Perez et al. 2012; Schweitzer et al. 2014), although some of this stress might have been due to the stress of social isolation itself (i.e. being isolated from other conspecifics). Breeding partners are often separated at the end of experiments and birds are kept in single-sex populations before pairing them at a later date with the same or a different partner for another experiment. In the wild, males and females form enduring partnerships and remain close to one another throughout the year (Mariette & Griffith 2012b) with little evidence of infidelity (Griffith et al. 2010) or divorce (Zann 1996). Hence, elevated stress hormones caused by partner separation or forced-pairing could contribute to reduced reproductive success in laboratories (see *Stress physiology*). There is also likely to be an effect on reproduction of the level of experience that a pair have in breeding together (Adkins-Regan & Tomaszycki 2007), and yet this is rarely reported or considered methodologically.

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

Variation in the size and construct of social groups (through housing, see Table 1) will also have consequences for the development of social and sexual behaviour in offspring (Rupoloh et al. 2012; Mariette et al. 2013). 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 (Holveck

Table 2: Reproductive success data from institutions (ordered alphabetically), from the perspective of females given the opportunity to breed

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[d]	Author
Arizona State University, USA	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, USA	D	I	Free	36	.	25	.	.	69	.	EA-R
Cornell University, USA	D	I	Free	16	.	14	13	3.92 ± 1.44	88	81	EA-R
Cornell University, USA	D	I	Free	64	.	.	31	2.68 ± 0.98	.	48	EA-R
Deakin University, Australia	W	O	Free	61	30	53	52	2.93 ± 1.13	87	85	MMM, KB
Deakin University, Australia	W	O	Free	37	7	35	23	2.72 ± 1.33	95	62	MMM, KB
Deakin University, Australia	W	O	Free	21	10	6	5	2.60 ± 0.89	29	24	MMM, KB
Instituto de Investigación en Recursos Cinegéticos, Spain	D	O	Free	41	33	40 in 177 attempts	37 in 137 out of 177 attempts	3.38 ± 1.24	98	90	AAR-H, CA-A
Instituto de Investigación en Recursos Cinegéticos, Spain	D	O	Free	44	27	42 in 198 attempts	42 in 133 out of 198 attempts	3.48 ± 1.41	95	95	AAR-H, CA-A
Instituto de Investigación en Recursos Cinegéticos, Spain	D	I	Forced	78	26	71 in 215 attempts	69 in 146 out of 215 attempts	3.24 ± 1.32	91	89	AAR-H, CA-A

Table 2 (Continued)

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[d]	Author
Instituto de Investigación en Recursos Cinegéticos, Spain	D	I	Forced	80	15	79 in 98 attempts	74 in 78 out of 98 attempts	4.11 ± 1.39	99	93	AAR-H, CA-A
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 mo)	D	I	Forced	11	10	11	8	1.88 ± 0.64	100	73	AN, MT
Lund University, Sweden (Experienced; ca 20 mo)	D	I	Forced	45	9.89 ± 2.49	45[e]	32	2.34 ± 1.12	100	71	AN, MT
Lund University, Sweden[f] (Experienced)	D	I	Forced	13	5	12	-	-	92	-	AN, MT
Lund University, Sweden[f] (Naive)	D	I	Forced	10	5	2	-	-	20	-	AN, MT
Macquarie University, Australia	W	O	Forced	40	10	34	21	3.14 ± 1.31	85	53	SCG
Macquarie University, Australia	W	O	Free	29	64	28	17	1.97 ± 0.68	97	59	LT, SCG, MCM
Macquarie University, Australia	D	O	Free	23	10	19	13	2.94 ± 1.09	83	56	LCM, SCG
Macquarie University, Australia (Naïve)	D	O	Forced	20	21	20	15	3.11 ± 1.57	100	75	LH, SCG
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

Table 2 (Continued)

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[d]	Author
Max Planck Institute for Ornithology, Seewiesen, Germany (Domestic from Sheffield; young females: 1.1 yrs)	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: 3.5 yrs)	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; 2 yrs)	W	O	Forced	36	18.48 ± 7.44	31	28	.	86	78	WF, MI
Max Planck Institute for Ornithology, Seewiesen, Germany (outbred; 0.8 yrs)	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: $F = 0.25$; 1.0 yrs)	W	O	Free (6:6)	18	13.03 ± 1.88	16	10	2.42 ± 0.96	89	56	WF, MI
Queen Mary University of London, UK	D	I	Free	34	18	33	29	2.86 ± 1.36	97	85	DFC, MM
Queen Mary University of London, UK	D	I	Free	11	8	10	10	3.30 ± 0.95	91	91	DFC, MM
Simon Fraser University, Canada (Experienced)	D		Forced	137	15 days to lay	129	66	3.34 ± 1.58	94	51	TDW
Simon Fraser University, Canada (Naive)	D		Forced	73	15 days to lay	56	29	3.85 ± 1.46	77	54	TDW
University of British Columbia, Canada	D	I	Forced	21	6–12	21	18	3.05 ± 1.76	100	86	NHP

Table 2 (Continued)

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[d]	Author
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[h]	26	4 wk to lay	25	17	3.76 ± 1.44	96	65	DLH, RN
University of Glasgow, UK (2007, Naïve)	D	I	Forced[h]	34	10 wk 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 wk to lay	33	-	-	87	-	DLH, RN
University of Glasgow, UK (age ca 7 mo)	D	I	Forced	117	12.87 ± 2.09	116	98	3.28 ± 1.23	99	84	VM, WB, PM
University of Glasgow, UK (age ca 43 mo)	D	I	Forced	27	4.12 ± 1.85	19	3	1.67 ± 1.15	70	11	VM, WB, PM
University of Glasgow, UK	D	I	Forced	101	14	81	65	3.45 ± 1.14	80	64	KAS, PM
University of Groningen, Netherlands	D	I	Forced	351 females in 1255 attempts	7.29 ± 4.38	332 females; 1132 of the 1255 attempts	228 females; 530 of the 1132 attempts with clutch	3.06 ± 1.50	95	65 overall; 42 attempts	MB, SV
University of Groningen, Netherlands	D	O	Free	52	112 ± 72.72	50 in 372 attempts with clutches	50 in 367 out of 372 attempts clutches	3.42 ± 1.79	96	96	MB, SV
University of Groningen, Netherlands	D	I	Forced	43	6	33	32	2.0 ± 1.18	77	74	KAS SV
University of Leiden, Netherlands – 2004	D	I	Forced	30[g]	10	16[i]	.	-	53	-	MJH, KR
University of Leiden, Netherlands – 2005	D	I	Forced	30[g]	10	22[i]	.	-	73	-	MJH, KR
University of Leiden, Netherlands – 2005	D	I	Forced[h]	11	10	11	8	4.00 ± 1.58	100	73	MJH, KR

Table 2 (Continued)

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^{d}	Author
University of Leiden, Netherlands – 2006	D	I	Forced^{h}	13	10	12^{i}	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, CV
University of Lyon/Saint-Etienne, France 2013 (Experienced)	D	I	Free	18	4	15	.	.	83	.	ICAB, ASV, CV
University of Lyon/Saint-Etienne, France 2013 (Experienced)	D	I	Free	12	4	12	.	.	100	.	ICAB, ASV, CV
University of Lyon/Saint-Etienne, France 2013 (Experienced)	D	I	Free	12	4	11	.	.	92	.	ICAB, ASV, CV
University of Montana	D	I	Free	12	31	9	9	4.53 ± 1.20	75	75	OLC
University of St. Andrews, UK	D	I	Forced	24	4	24	13	3.00 ± 1.41	100	54	NB
University of St. Andrews, UK	D	I	Forced	26	10	24	18	3.00 ± 1.14	92	69	LG, IB, SH
University of St. Andrews, UK	D	I	Forced	9	9	7	6	3.33 ± 1.21	78	67	LG, IB, SH
University of St. Andrews, UK	D	I	Forced	10	10	8	8	3.38 ± 1.18	80	80	LG, IB, SH
University of St. Andrews, UK	D	I	Free (12:12)	25	8	24	23	3.57 ± 1.38	96	92	KAS MGE

Table 2 (Continued)

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[d]	Author
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, USA	D	I	Forced	18	52	18 in 212 attempts	15	1.39 ± 1.99	100	83 overall; 39% of attempts	CVR, JPS

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

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

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

[d] The percentage out of all females given the opportunity.

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

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

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

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

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

et al. 2008; Brumm et al. 2009) 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 & 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 (Riebel 2009; Bolund et al. 2012; 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; Riebel et al. 2009; Honarmand et al. 2015), and therefore potentially this may vary systematically across populations.

Humidity and temperature

In wild zebra finches, the trigger of breeding activity has generally been related to rainfall (Zann et al. 1995). Other environmental cues such as humidity and temperature have been shown to both directly (Vleck & Priedkalns 1985; Cynx 2001) 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 groundwater 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 (1996b) considered humidity range of 35–55% as constant. Williamson et al. (2008) found seasonal patterns of maternal investment in birds breeding in ‘constant temperature and humidity rooms’ but suggest that the 40–60% variation in humidity in their study may have been the variable that could have influenced breeding if the birds are sensitive to such changes. Therefore, it appears important to pay attention to even small changes in humidity, as there remains the possibility that variation in humidity in captive breeding environments may affect reproductive output. Unfortunately, it is very difficult to artificially control humidity to a high degree as air-heating systems typically deliver dry air, and humidity is not often controlled to a high level of precision independently of air temperature.

In addition to humidity, variation in temperature is likely to affect reproductive physiology and behaviour in ways that may contribute to variation in reproductive success. Wild zebra finches have been recorded breeding throughout the winter in temperatures as low as 2.2°C (Zann et al. 1995), and in summer in temperatures above 40°C (Griffith et al. 2016). Periods of low temperature are associated with a reduction or cessation of reproductive activity in wild zebra finches (Davies 1977). Reproductive success in captive birds may be similarly affected by variation in temperature, or across seasons. Captive birds kept at low temperature (7°C) increased food consumption and time to initiate egg laying and decreased the total number of eggs laid (Salvante et al. 2007). Furthermore, presumably due to the costs of thermoregulation, females reduce the amount of heat transferred to eggs during incubation in low temperature conditions (Nord et al. 2010). The standardized and invariant climatic conditions of captive studies may cause their own problems, but it is worth noting that studies of wild birds generally also rarely report the climatic conditions during which ecological studies are conducted, and these are also likely to cause variation across studies.

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

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 et al. 1998; Pariser et al. 2010).

Part III. Variation in Reproductive Success Across Laboratories

Here, we characterize the variation across laboratories in the reproductive success of individuals breeding in different contexts. The data we present are unsuitable for directly measuring the extent of selection (because they do not represent lifetime reproductive success). However, they provide a first indication of the extent to which selection might be acting in such populations and also on interpopulation differences. The level of contemporary selection may also affect the composition of experimental data sets. For example, variation between pairs in the latency to lay (when presented with an opportunity to breed) results in a selective pressure determined by the amount of time birds are given to breed. 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 (such as bill colour, or prior breeding experience). If such relationships exist then, for example, if the research focuses on parental care, then the data will be gathered only on the subset of birds that have bred before the experimental cut-off is reached. It will also affect the composition of subsequent generations if the cut-off determines which individuals produce offspring and which do not. There are anecdotal reports that finch breeders only breed females that lay eggs quickly when given a mate, and this may have resulted in selection over many generations of domestication. There are many logistical reasons why experimental cut-offs are used, and we simply wish to raise an awareness of the sort of bias that they may introduce.

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

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 10 years to request their involvement in this study. A number of researchers did not respond to this initial communication and are therefore not represented, along with other researchers that were unable to, or did not wish to contribute data on these specific questions. The authors of this paper have contributed their own data where applicable and contributed to the writing of the paper. Data were compiled in an effort to determine the proportion of females that produce (1) eggs and (2) fledglings, when given the opportunity to breed (Table 2). For these same pairs, we also report whether they were housed in a cage or aviary, whether they were force-paired or free to choose partners, as well as whether they originated from wild or domestic stock. Contributors provided data from their records, and none of these data were the result of work targeted just at assessing proportional reproductive success. These breeding data were collected as part of researchers' independent ongoing research with this species, which was conducted in line with their own animal ethics approvals and the legal requirements of their respective countries. We collated data from situations in which birds were not subject to experimental manipulations that are likely to have significantly affected their reproduction. In cases in which broods had been switched in cross-fostering experimental designs, we used only the data collected up to the point of the cross-fostering. Most of the data we have gathered and presented come from individuals given a single opportunity to breed. However, we have included a focus on one of the studies in which individuals were allowed to breed repeatedly over an extended period of time. These data (provided by Varian-Ramos and Swaddle, from the College of William & Mary, United States, summarized in Table 3) provide us with an excellent opportunity to assess the repeatability of reproductive success at an individual level. These data provide important insight into the extent to which reproductive success and failure may be attributable to individual differences. In their study, Varian-Ramos et al. (2014) tracked a total of 33 individuals over a 12-month period in which the birds were allowed to breed *ad libitum*. We used only the data from the control individuals in that study, as those birds were not subject to the experimental treatment that was the focus of that work (Varian-Ramos et al. 2014). Varian-Ramos et al. (2014) removed clutches 21 days after the last 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. The removed clutch was excluded from analyses, and similarly 12 broods were removed immediately after fledgling and these were excluded from the analysis of those offspring reaching independence.

Table 3: Breeding data from 33 females that were given freedom to breed over a 12-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	NA
121	14	70	5	0	7.1	0.0
300	13	33	0	0	0.0	NA
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

Statistical Methods

Our statistical analyses were focused on addressing individual repeatability of reproductive success, and characterizing variation in reproductive success across and within populations, as well as investigating a couple of likely factors that might determine that variation. The percentage of females in each study that succeeded in clutch initiation and producing at least one fledgling in the across-study data set, and the percentage of breeding attempts per female that were successful in producing either fledglings or independent young in the data from the College of William & Mary, US; CW Varian-Ramos and JP Swaddle (Table 3) were transformed into binary data (i.e. 1: success, 0: failure) for all the analyses. Intraclass correlation (ICC) was calculated for this success–failure outcome to examine the variability of reproductive success at the level of individual (data from: Varian-Ramos et al. 2014). The ICC in latent scale (link scale) was estimated based on generalized linear mixed models (GLMMs) 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). The models included identity of female as a random effect. Differences between ICC estimates were examined based on posterior probability. Models were fitted, and parameters were estimated with Markov chain Monte Carlo, using software Stan (http://mc-stan.org/) called from the R package rstan (Stan Development Team 2016). Female identity effects on clutch size, the number of fledglings and independent young were tested using a generalized linear model (GLM). The difference between females (those who produced at least one fledgling) in the number of fledglings was examined with a zero-inflated Poisson (ZIP) model with log and logit link functions using R package pscl (Zeileis et al. 2008).

The effect of several factors on clutch initiation and fledging success was investigated using two separate GLMM with a binomial distribution and logit link function. In both cases, housing condition (indoor vs. outdoor), pairing type (forced vs. free choice) and origin of strain (captive-bred vs. wild-derived) were included as fixed effects. Identity of study and identity of institution were included as random effects. Models were fitted using R package lme4 (Bates et al. 2015). Similarly, the effects of female age were examined using GLM with a binomial distribution and logit link function.

Results

Individual Repeatability in Reproductive Success

In the data reported in Table 3, for a set of females over a period of continual breeding (52 wk) 33 females produced 316 clutches (mean = 9.58 ± 2.99 SD). In total, 1670 eggs were laid (mean clutch size 5.32 ± 1.62 SD) and from these eggs 704 chicks hatched (mean per clutch 2.55 ± 1.66 SD). From these chicks, 544 birds were fledged (mean per clutch 2.00 ± 1.52 SD; mean per female 16.48 ± 9.69 SD) and 461 independent were produced (mean per clutch 1.82 ± 1.51 SD). Overall just 42% of all eggs laid went on to hatch and just 28% of eggs produced an offspring that survived to independence. The relationship between the number of fledglings produced in each nest (not accounting for female ID) and the number of independent offspring produced was strong ($r^2 = 0.87$, df = 138, t-value = 30.07, $p < 0.001$). However, the relationship 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 relationship 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 clutch size (likelihood ratio test, $\chi^2 = 126.65$, df = 34, $p < 0.001$, n = 380 nests, GLM), likelihood of successfully producing fledglings (categorized as a binary variable) ($\chi^2 = 171.7$, df = 32, $p < 0.001$, n = 316, GLM), 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), ZIP model, and in the likelihood of producing independent offspring (categorized as a binary variable) ($\chi^2 = 159.9$, df = 32, $p < 0.001$, n = 304, GLM); See Fig. 1b]. The proportion of variation explained by interfemale differences did not differ for the success in rearing young to fledging, and in rearing them to independence (for the production of fledglings, Intraclass correlation (ICC) = 0.56, SE = 0.095, n = 316 nests; and for independent offspring, ICC = 0.53, SE = 0.094, n = 304; posterior probability, Pr(fledging < independence) = 0.45). Both variables were more repeatable than clutch size (ICC = 0.22, SE = 0.058, Pr(fledging < clutch) = 0.0, Pr(independence < clutch) = 0.004).

Cross-Study Comparison of Clutch and Fledging Success

From Table 2, we combined data from 23 institutions on egg hatching success per female and from

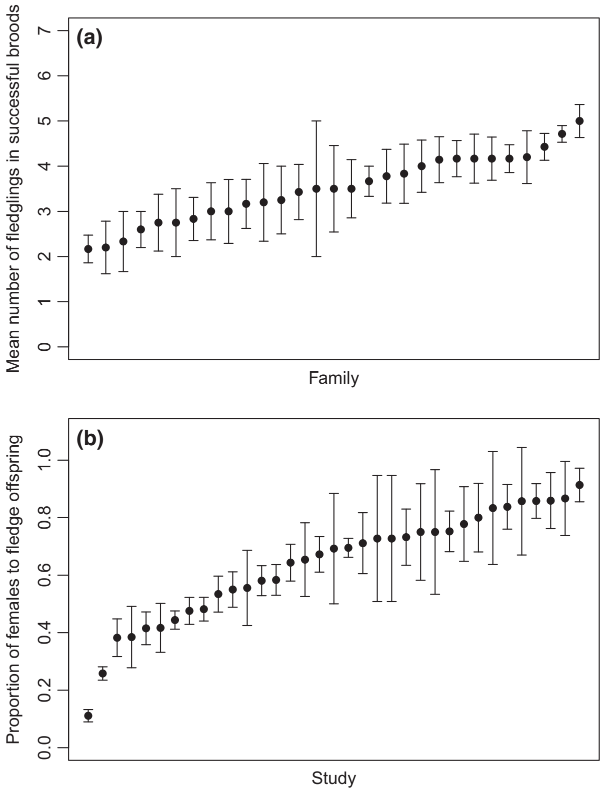

Fig. 1: (a) Mean number (±SE) of fledglings produced per successful brood across 29 females that were given the opportunity to breed repeatedly across a year, and that raised at least some fledglings successfully (four females failed to fledge any offspring and are therefore not represented). All 29 females were successful but there are significant differences in how many fledglings they produced (see results). All data were from the longitudinal study by Varian-Ramos et al. (2014). (b) The proportion of females (±SE) that successfully fledged offspring when given the opportunity to breed. Data from 35 studies.

21 institutions on fledgling rearing success per female. In total, 2813 females of 3213 successfully hatched chicks (proportion = 0.88, SE = 0.006), and 1899 females of 2906 raised fledglings (proportion = 0.65, SE = 0.01). The probability of females initiating at least one clutch varied across studies ($\chi^2 = 136.96$, df = 1, $p < 0.001$, n = 3213 females, 70 studies, 23 institutions, GLMM) but not across institutions ($\chi^2 = 0.0008$, df = 1, p = 0.98). Similarly, the probability of producing fledglings was different across studies ($\chi^2 = 136.78$, df = 1, $p < 0.001$, n = 2906 females, 57 studies, 21 institutions, GLMM, Fig. 1b) but not across institutions ($\chi^2 = 2.5$, df = 1, p = 0.11), suggesting that experimental conditions specific to individual studies explain more variation in egg laying than population-level factors.

Reproduction and Pair and Female Characteristics

Females were as likely to produce a clutch when housed either indoors or outdoors (Wald test, $z = 1.65$, p = 0.099, n = 3003 females, n = 68 studies, n = 20 institutions, GLMM; Fig. 2a), and when force-paired or given free choice of partner ($z = 0.25$, p = 0.8; Fig. 2b), while a higher proportion of females from domestic origin produced a clutch than those from wild-derived populations ($z = -2.08$, p = 0.04; Fig. 2c). Females in indoor cages fledged significantly fewer young than did females breeding in outdoor cages/aviaries ($z = 2.42$, p = 0.016, n = 2696 females, 55 studies, 22 institutions, GLMM; Fig. 2d). Females from domesticated strains were more likely to produce fledglings than those in populations derived from the wild more recently ($z = -3.65$, $p < 0.001$; Fig. 2e). 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; Fig. 2f). For three institutions, we could compare success of females from two different age categories (all else is presumed to be equal). In two of the three institutions, young females had a greater reproductive success than older ones. In Lund, Sweden, domesticated females (females of 9 vs. 20 mo) 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, GLM). In domesticated birds in Glasgow, UK, (females of 7 vs. 43 mo) younger females were more likely to produce a clutch ($z = 3.57$, $p < 0.001$, n = 144, GLM), and to fledge young ($z = 5.62$, $p < 0.001$, n = 144, GLM). At the Max Planck Institute (Seewiesen, Germany), there were comparative age classes across both domesticated and wild-derived birds, allowing two separate comparisons. For domesticated birds (13 vs. 42 mo), young birds were more successful at producing clutches ($z = -4.214$, $p < 0.001$, n = 328, GLM) and in fledging offspring ($z = -5.437$, $p < 0.001$, n = 328, GLM). For wild-derived birds (10 vs. 24 mo), young females also tended to be better at producing clutches ($z = -1.028$, p = 0.30, n = 114, GLM) and fledglings ($z = -1.073$, p = 0.28, n = 114, GLM).

Discussion

We found that a significant percentage (around 35%) of females do not successfully produce offspring when given the opportunity to breed in the captive context. Approximately half of these females fail to produce a clutch, and the remainder did not successfully raise offspring. For those females that do produce a clutch,

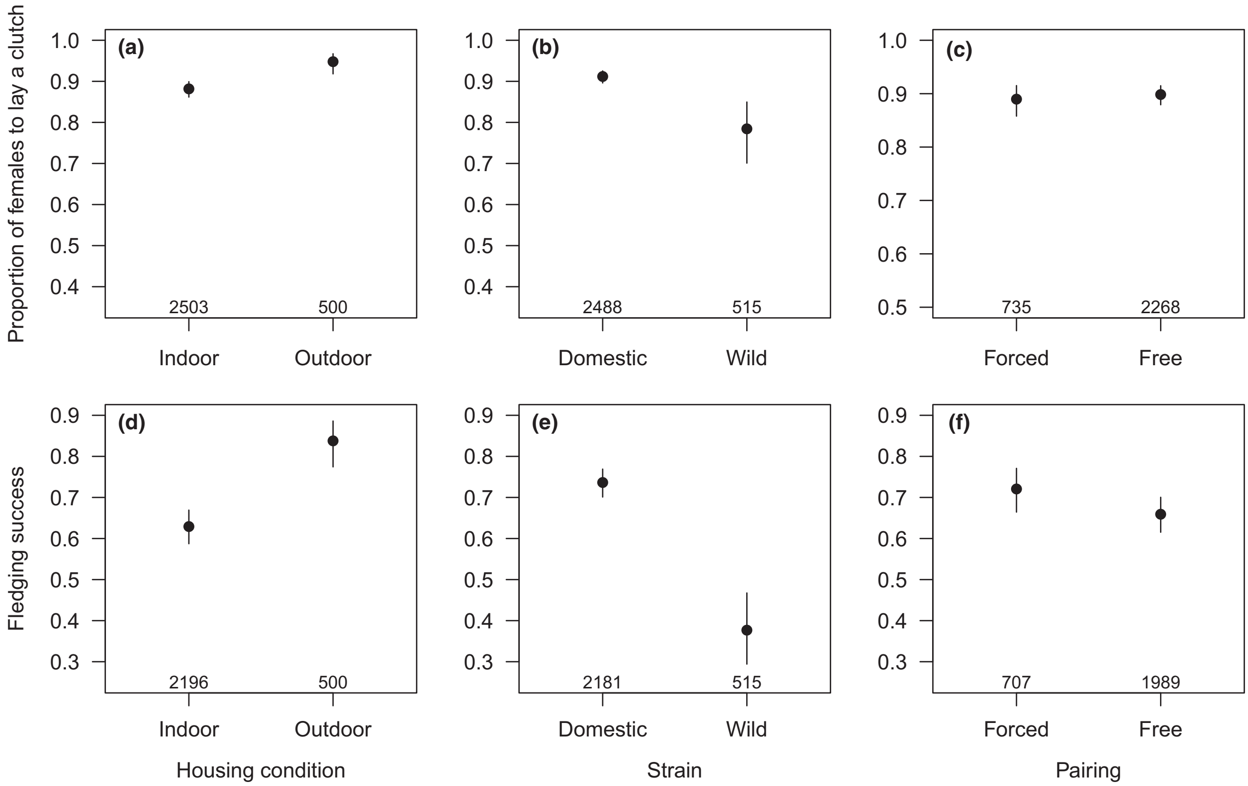

Fig. 2: The reproductive output of females when given the opportunity to breed measured through two metrics: producing a clutch (a–c), and producing fledglings (d–f). Females were examined across two categories: either housed indoors or outdoors (a and d); domestic or wild origin (b and e); force-paired or free choice (c and f). The graphs show predicted mean (±SE) from GLMM. The numbers on the graphs are the number of females used.

the primary determinant of reproductive failure is hatching failure. However, these birds also fail to raise hatched nestlings to fledging and in the subsequent production of independent young. Most of this variation is driven by differences across individual studies rather than differences across institutions. On the one hand, this may perhaps be comforting because it suggests that generally laboratory populations are not hugely different from one another in the way in which they reproduce. However, this does also suggest that variation in reproduction can be driven by the differences in the way that individual studies are set up and that certainly is a cause for concern, because it means that the replicability of results may be challenging even with the same set of birds, if, as yet-unidentified parameters are changed between studies. We suggest that future studies try to identify which of the parameters we have reviewed in Parts I and II are the cause of this interstudy variation.

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 were data available (the age of young and old females varied across the studies – see results). 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. We also found that females that bred outdoors produced a higher number of fledglings than those that bred indoors although those categories also typically correlate with the size of the breeding enclosure (cages vs. aviaries). Again, this finding from the data overall is not from controlled studies designed to test for this difference specifically. We found no evidence of a difference between females that were force-paired, or those that were free to choose their partner (but see Ihle et al. 2015 for a more direct investigation of this that found an effect).

We also found some evidence for a higher level of reproductive success in domesticated birds than in laboratory populations that were recently derived from birds taken from the wild. 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 intraclass correlation in reproductive success at the level of individual females, indicating that individual reproductive success was repeatable in the longitudinal data from the College of William and Mary (Table 3, Fig. 1a). The latter data also illustrate how strong the selection can be, with a large reproductive skew across the females monitored (although of course some of this may have been due to their mate).

It is important to be mindful that the data presented here were not originally collected in order to address these issues. The heterogeneity in the data sets presented and in the context in which the captive populations were held precludes a comprehensive investigation into the sources of variation in breeding success among these research laboratories. Nevertheless, we believe it is worthwhile to consider and highlight the potential sources of variation that might

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

Aspect	Item	Detail
Study design	N experimental groups	
	N control groups	
	Nature of replication	For example, whole experiment was conducted twice
Numbers used	N adult males used	(count all individuals that were initially used)
	N adult females used	
	N males with opportunity to reproduce	
	N females with opportunity to reproduce	
	N females that laid eggs	
	N females that had chicks	
	N females that fledged young	
	N males for which data is presented	
	N females for which data is presented	
	N individuals that died or removed	For example, one bird was removed after injuring a wing
	Other reasons for missing data	For example, some blood samples not assayed
Experimental procedures	Nature of any experimental manipulation	Specify details (i.e. testosterone implant)
	Nature of any invasive work	For example, 30 μl blood sample during chick rearing
	Duration given for breeding opportunity	For example, 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	For example, force-paired or free choice
	Any bias in selection of individuals	For example, only birds with breeding experience used
Housing and husbandry	Cage/aviary size	Width × length × height (m)
	N individuals per cage	
	Sex ratio present in each cage	For example, 0.5 (as many males as females)
	Food provided *ad libitum*	For example, dry seed finch mix
	Supplemental food provided	Type and frequency
	Any restriction in provision of food	For example, seed provided mixed with husk
	Type of nest site provided	For example, wooden nest box, woven basket
	Nesting material provided	For example, Hessian fibre, coconut fibre, feathers, grass
	Environmental enrichment or shelter	For example, shelter in 1/3 of cage
	Indoors or outside	
	Temperature control	For example, constant 25°C, or local outside conditions
	Humidity control	For example, 50%
	Light/dark cycle	For example, 14L:10D
Results – baseline data	Average clutch size	Mean ± SD
	Average number of fledglings	Mean ± SD (excluding zeros)

contribute, at least in part, to variation within and between populations in reproductive success of domesticated zebra finches.

Summary

The ease with which domesticated zebra finches breed in captivity, relative to other birds, has made them a model system for research across a diversity of fields. The zebra finch will remain 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. We present data showing a large amount of variation in reproductive success across research laboratories. Although this variation is often noted anecdotally, it has not been the focus of any studies to date. Here, we have highlighted several potential factors that often vary between laboratories that could influence variation in reproductive success in domesticated zebra finches.

We accept that there is always likely to be variation in the housing and husbandry practices of different laboratories. Research groups have to make strategic decisions on the basis of space or monetary constraints as well as following different opportunities to optimize local welfare recommendations. However, for some of the parameters examined, there is no obvious reason why some conditions could not be more standardized. For example in Table 1, we can see that most studies are conducted with a day:night ratio of 14:10 h, and around 22°C. Perhaps these could be taken by future studies as standard conditions, which would start to reduce the heterogeneity among different studies? Although more standardized conditions across laboratories might be the most desired outcome, at the least we suggest that further consideration should be given to the way heterogeneity in conditions and protocols across different studies may affect outcomes. This may provide insight into why laboratories can find conflicting results when approaching similar questions in the same species (Jennions 1998; Seguin & Forstmeier 2012).

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

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

Recommendation

We propose that all future work on captive zebra finches includes the information itemized in Table 4. While some of that information might be considered quite standard information, much of it is not reported in papers focused on captive zebra finches. We suggest that these data could be presented in a Table provided either in the Methods section or as Supplementary material. The information requested in Table 4 is heavily informed by the items outlined in Kilkenny et al.'s (2010) ARRIVE Guidelines and their Table 2 with some additional information that is more relevant to the zebra finch (as discussed above). We advocate that the table be completed and used as is, rather than being modified with fields excluded or additional ones included. A standardized reporting form will facilitate future efforts to harvest and utilize the material presented.

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