

Experimental dissociation of the effects of diet, age and breeding experience on primary reproductive effort in zebra finches *Taeniopygia guttata*

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Reproductive performance varies with age in a wide range of organisms, and increasingly such patterns are interpreted in terms of state-dependent models. We sought to characterise 'state' with regards to age-related variation in clutch size, egg mass and timing of breeding in captive zebra finches *Taeniopygia guttata*, focusing on the roles of diet quality, age and breeding experience. Females on a high-quality diet laid larger clutches of larger eggs than did females on a low-quality diet. The effect of age on reproductive performance was examined by comparing females breeding (i.e. paired) for the first time at either 3- and/or 6-months of age. Clutch size increased with age but on the low-quality diet only, not on the high-quality diet. Furthermore, clutch size *decreased* between 3- and 6-months of age in birds bred first on the high-quality diet and then on the low-quality diet. Age did not affect egg mass but older birds had shorter laying intervals. Reproductive performance did not differ between females breeding at 6-months of age for the first or second time: the effects of age were not due to 'training' effects or experience specific to breeding (e.g. undergoing the physiological process of egg formation). In conclusion, nutritional condition (diet) emerged as a central component of state that could strongly influence, and even reverse, any age-dependent increase in primary reproductive performance.

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Age-specific patterns of reproduction are common to most long-lived, iteroparous animals with reproductive performance typically increasing with age, at least until some intermediate age after which senescence may occur (Clutton-Brock 1988, 1991, Newton 1989, Stearns 1992). McNamara and Houston (1996) argue that such life-history patterns are best understood in terms of state-dependent models that allow for variation between individuals, rather than strictly age-based approaches that assume that all individuals of a given age are equivalent (see also Boyd 2000). For instance, if reproductive effort is determined by nutritional condition and condition is correlated with age, reproductive performance will vary with age even when there is no

effect of age *per se* (McNamara and Houston 1996); in such a scenario, condition (or diet) is the biologically relevant parameter, not age. An important component of the state-dependent approach is that it is crucial to identify the factors that determine 'state' in order to devise empirical tests of the theory (Morris 1996, 1998). Characterising state for a given life-history trait will not simply consist of listing relevant variables (e.g. mass, nutritional status), but will also require identifying the interactions between them (i.e. how the effect of one factor depends on another; Morris 1996, 1998).

Age-specific patterns of reproduction have been documented extensively in avian species (Saether 1990, Forslund and Pärt 1995, Christians 2002) but few stud-

ies have examined the mechanisms underlying these patterns (Martin 1995). Three major explanations have been proposed to explain these patterns: a) age-related improvements in competence, the “constraint” hypothesis, b) optimisation of reproductive effort, the “restraint” hypothesis, and c) the progressive appearance and disappearance of different phenotypes in the breeding population, the “selection” hypothesis (Perdeck and Cave 1992, Forslund and Pärt 1995, Martin 1995). Proximate factors that might limit reproduction in young birds include foraging efficiency (Desrochers 1992a, b) and physiological maturation (Robertson et al. 1994, Ottinger et al. 1995), although few studies have provided good evidence for physiological constraints. In either case, improvements with age might be due to either changes in general skills or physiological traits (i.e., age *per se*) or to a ‘training effect’ specifically associated with the act of breeding (i.e., experience).

Primary female reproductive effort (i.e. timing of laying, egg and clutch size) increases with age in a variety of avian species (e.g. Cooke et al. 1995, Hipfner et al. 1997, Daunt et al. 1999; see Saether 1990, Perdeck and Cave 1992 for earlier reviews). In our study, we sought to identify elements of ‘state’ that are responsible for this age-related variation in captive zebra finches *Taeniopygia guttata*, focusing on the roles of diet quality (Selman and Houston 1996, Birkhead et al. 1999), age and prior breeding experience. We primarily focus on the “constraint” hypothesis, i.e. age-dependent changes in individual birds, by analysing females which successfully laid eggs at both a younger and an older age. To investigate the role of nutrition, we compared females breeding on a low-quality seed diet with those breeding on a high-quality diet of seed supplemented with hen’s egg. The effect of age was examined by comparing females which were paired and bred for the first time at either 3- or 6-months of age. The effect of prior breeding experience was assessed by comparing females breeding at 6-months of age for the first or second time. We also examined interactions between nutrition, age and experience by varying the diet of some individuals between breeding attempts. In addition to the three factors that were manipulated experimentally, we examined the mass of the female when she fledged as a potential source of between-individual variation, since previous studies have suggested that environmental conditions early in life may have lasting effects on reproductive performance (Haywood and Perrins 1992, Hørak 1994, Potti 1999).

Materials and methods

Experiments and animal husbandry were carried out under a Simon Fraser University Animal Care Commit-

tee permit (# 399B), in accordance with guidelines from the Canadian Committee on Animal Care (CCAC). Zebra finches were maintained and bred in controlled environmental conditions (temperature 19–23°C, humidity 35–55%, constant light schedule = 14L:10D, lights on at 07.00 PST). All birds were provided with a mixed seed diet (panicum and white millet, 1:3, 11.7% protein, 0.6% lipid and 84.3% carbohydrate by dry mass; Williams 1996b), water, grit and cuttlefish bone (calcium) *ad lib* and received a multi-vitamin supplement in the drinking water once per week. Breeding pairs were housed individually in cages (61 × 46 × 41 cm) each with an external nest box (11.5 × 11.5 × 11.5 cm). Females were weighed (± 0.1 g) at the time of pairing with a male. Nest boxes were checked daily between 09.00 and 11.00 and all new eggs were weighed (± 0.001 g) and numbered to obtain data on egg size, clutch size and laying interval (the time between pairing and laying of the first egg). If no new eggs were laid over two days the clutch was considered to be complete (< 1% of birds lay subsequent eggs at > 2 day intervals) and birds were returned to non-breeding communal cages with a seed-only diet, i.e. birds were not allowed to incubate eggs or rear chicks. Any female not laying within 15 days of pairing was considered a non-breeder.

Many females used in this study were bred in-house and were weighed at 21-days of age, shortly after they ‘fledged’ (i.e. left the nest box). Thus, ‘fledging mass’ is a trait of the adult females used in this experiment and refers to their mass at 21-days of age. These data were not available for all individuals as some birds were purchased when they were 2-months old (these birds were aged ± 1 week based on the black colour of the bill; Zaan 1996).

Due to the complexity of the experimental design, and the large number of birds of specific ages that were required, breeding experiments were carried out, in part, sequentially, and at two different breeding facilities (Simon Fraser University, and the Department of Animal and Plant Sciences, University of Sheffield, UK). However, a) all females were bred under the same controlled conditions (see above), b) for group (1), see below, we had birds bred at both locations and there was no significant ‘site’ difference for mean egg mass, clutch size or laying interval ($P > 0.10$ in all cases), and c) we have shown elsewhere that experiments conducted at the two locations produce replicable results, e.g. compare Williams (1996a, b) with Balzer and Williams (1998), and Salvante and Williams (2002). At 3-months of age, females were assigned to one of three groups: (1) breeding at 3- and 6-months on a low-quality diet (i.e. seed diet described above; $n = 16$), (2) breeding at 3- and 6-months on a high-quality diet (i.e. seed plus a daily supplement of 6 g hen’s egg, consisting of 20.3% protein and 6.6% lipid, starting on the day of pairing and provided in a small dish on the cage floor; $n = 10$),

and (3) breeding at 3-months on the high-quality diet and at 6-months on the low-quality diet ($n = 12$). We chose the latter treatment, because the converse treatment of a low-quality then high-quality would intuitively be confounded by any age-dependent improvement in reproduction between breeding attempts. In addition, two further groups of birds were kept in single sex communal cages on the seed-diet until 6-months of age and then they were bred for the first time on either (4) the low-quality diet ($n = 13$), or (5) the high-quality diet ($n = 9$), i.e. these birds were chosen randomly and were prevented from breeding at 3-months. We also randomly selected only one daughter per brood to be included in the analysis for any experimental group. However, all females from each communal cage were paired (so there was no bias introduced by capture order; see also Birkhead et al. 1998). All females were paired and bred with experienced males > 6 months of age (i.e. males which had been previously paired with females that produced eggs) and males were assigned to pairs randomly.

Only females that produced at least one egg at both 3- and 6-months (groups 1–3) or at least one egg in their first breeding attempt (groups 4 and 5) were included in our main analyses. Thus all females in groups 1–3 were “experienced” at 6-months. All statistical analyses were carried out using general linear models (proc GLM; SAS Institute 1990); body mass at pairing was initially included in each model, but was removed if not significant ($P > 0.05$). Values are presented as least-squares means \pm SE unless stated otherwise.

Results

Our study was not specifically designed to test the selection hypothesis (*sensu* Forslund and Pärt 1995), i.e. the effect on population mean reproductive trait values of the appearance or disappearance of different phenotypes in the breeding population: we primarily focussed on birds that bred at both 3- and 6-months of age (see subsequent analyses). However, some females failed to lay eggs when first paired at 3-months of age (all birds first paired at 6-months of age laid eggs, and no bird laying at 3-months failed to lay at 6-months). We have breeding records for some of these females which subsequently bred in our colony on the low quality seed diet ($n = 11$ birds). We therefore compared reproductive trait values for these females with those from the 6-month breeding attempt on the seed diet for females which bred at both 3- and 6-months of age ($n = 29$; Table 1). There was no difference in body mass at pairing, clutch size or laying interval between these two groups ($P > 0.25$ in all cases), but females which failed to breed at 3-months of age laid smaller eggs in their subsequent breeding attempt ($F_{1,39} = 8.01$, $P < 0.01$;

Table 1. Reproductive trait values at 6-months of age on a low-quality seed diet for birds which either did or did not lay eggs when first paired at 3-months of age. Values are means \pm S.E.; asterisks (**) indicate significant differences ($P < 0.01$).

Reproductive trait	No eggs at 3-months ($n = 11$)	Eggs at 3-months ($n = 29$)
Body mass at pairing (g)	16.1 \pm 0.7	16.9 \pm 0.4
Mean egg mass (g)	0.943 \pm 0.029	1.039 \pm 0.018**
Clutch size	3.8 \pm 0.4	4.1 \pm 0.3
Laying interval (days)	6.00 \pm 0.5	5.3 \pm 0.3

Table 1). There was no effect of the 3-month breeding diet on the proportion of birds which did not lay eggs (low quality diet, 15.5% vs. high-quality diet, 6.8%; Fishers Exact Probability test, $P > 0.10$).

Effect of diet quality and interactions with age/experience

The following analyses included only birds that bred at both 3- and 6-months of age (i.e. groups 1–3). Clutch size, egg mass and laying interval were all influenced by diet (Table 2, Fig. 1). Females on the higher-quality, egg-supplemented diet laid more eggs than birds on the lower-quality seed diet at 3-months of age ($F_{1,36} = 16.13$, $P < 0.001$) and at 6-months of age ($F_{1,36} = 7.51$, $P < 0.01$). Similarly, females on the high-quality diet laid heavier eggs than birds on the low-quality diet at 3-months of age ($F_{1,35} = 6.07$, $P = 0.02$, controlling for body mass) and at 6-months of age ($F_{1,35} = 6.00$, $P = 0.02$, controlling for body mass). In contrast to clutch size and egg mass, laying interval was independent of diet in birds breeding at 3-months of age ($F_{1,35} = 2.31$, $P > 0.10$, controlling for body mass), but at 6-months it was longer in birds on the high-quality diet compared with birds on the low-quality diet ($F_{1,36} = 5.01$, $P = 0.03$).

Diet also influenced the effect of age/experience on reproductive performance (Fig. 1; age and experience were confounded in these analyses since only females bred at 3- and 6-months of age were included). Clutch size did not differ between 3- and 6-months of age in birds maintained on the high-quality diet (paired test: $F_{1,9} = 1.98$, $P > 0.15$) or the low-quality diet ($F_{1,15} = 2.72$, $P > 0.10$). However, clutch size decreased significantly in birds transferred from the high- to low-quality diet between 3- and 6 months of age ($F_{1,11} = 6.17$, $P = 0.03$; Fig. 1). Egg mass showed a similar pattern, i.e., there was no difference between 3- and 6-months of age in birds maintained on the high-quality diet ($F_{1,9} = 1.63$, $P > 0.20$) or on the low-quality diet ($F_{1,15} = 2.41$, $P > 0.10$), but there was a significant decrease in egg

Table 2. Effects of age/experience and diet on primary reproductive effort in female zebra finches breeding at 3- and 6-months of age (analysis includes only birds that bred at both 3- and 6-months of age).

Reproductive trait	Source of variation	df	MS ^a	F	P
Clutch size	Diet	1	7.882	6.32	0.017
	Age/experience	1	0.004	0.00	0.953
	Diet × Age/experience	1	4.158	3.34	0.076
	Individual female	37	2.551	2.05	0.018
Egg mass	Diet	1	0.036	6.09	0.019
	Age/experience	1	0.005	0.78	0.376
	Diet × Age/experience	1	0.019	3.16	0.084
	Individual female	37	0.023	3.94	0.001
Laying interval	Diet	1	12.061	5.95	0.020
	Age/experience	1	25.432	12.54	0.001
	Diet × Age/experience	1	5.444	5.34	0.027
	Individual female	37	10.817	2.69	0.002

^a Derived from partial (Type III) sums of squares.

mass in birds transferred from the high- to low-quality diet between 3- and 6-months of age ($F_{1,10} = 25.7$, $P < 0.001$, controlling for body mass; Fig. 1).

In contrast to clutch size and egg mass, laying interval decreased significantly with increasing age/experience both in birds maintained on the low-quality diet ($F_{1,15} = 17.4$, $P < 0.001$) and in those transferred from the high- to low-quality diet ($F_{1,11} = 74.9$, $P < 0.001$). However, laying interval did not change with age/experience in birds maintained on the high-quality diet ($F_{1,9} = 0.48$, $P > 0.20$).

Effect of age

To investigate the effect of age *per se* we compared birds breeding for the first time at 6-months of age with those breeding for the first time at 3-months, with age (3- or 6-months), diet (low- or high-quality diet) and the age × diet interaction as terms in a general linear model. The interaction between age and diet was significant for clutch size ($F_{1,56} = 4.17$, $P = 0.05$) and therefore we analysed data from the two diets separately. Clutch size at first breeding increased with age on the low-quality diet ($F_{1,27} = 6.41$, $P = 0.02$), but not on the high-quality diet ($F_{1,29} = 0.29$, $P > 0.20$; Table 3).

There was no significant interaction between age and diet in the analysis of egg mass ($F_{1,55} = 0.04$, $P > 0.20$) and therefore the interaction term was removed from the model. There was no effect of age on egg mass ($F_{1,56} = 0.72$, $P > 0.20$, controlling for body mass). As in the previous analysis, egg mass at first breeding was dependent on diet ($F_{1,56} = 6.55$, $P = 0.01$, controlling for body mass), with females on the high-quality diet producing larger eggs (Table 3).

For laying interval, as with egg mass, the interaction between age and diet was not significant ($F_{1,56} = 0.90$, $P > 0.20$), so the interaction term was dropped from the model. There was a significant effect of age on laying

interval ($F_{1,57} = 5.25$, $P = 0.03$), with 6-month old birds having shorter laying intervals than 3-month old birds (Table 3). Diet did not have a significant effect on laying interval of females breeding for the first time ($F_{1,57} = 0.09$, $P > 0.20$), thus confirming our previous analysis.

Effect of prior breeding experience

To investigate the effect of experience *per se* we examined 6-month old birds breeding for their first or second time. The experience × diet interaction term was not significant for clutch size or egg mass ($P > 0.20$ in both cases) and was not included in the model. Experience did not have a significant effect on clutch size ($F_{1,57} = 2.34$, $P > 0.10$), egg mass ($F_{1,56} = 0.30$, $P > 0.20$, controlling for body mass), or laying interval ($F_{1,57} = 2.16$, $P > 0.10$) at 6-months (Table 3). However, diet did have significant effects on all three parameters, with females on the high-quality diet laying larger clutches of larger eggs, but having longer laying intervals, again confirming our previous analyses (Table 3).

Effect of body mass at fledging

There was highly significant variation between individual females in all three reproductive traits ($P < 0.02$ in all cases), even after accounting for the effects of diet, age, and experience (Table 2). We therefore examined the effect of body mass at fledging as a potential source of this variation. Mean fledging mass for these birds was 12.0 ± 0.9 g ($n = 23$), mass at pairing at 3-months of age was 15.6 ± 1.7 g, and these traits were positively correlated ($r = 0.55$, $P < 0.01$). Among females bred at both 3- and 6-months we found no relationship between body mass at fledging and clutch size, egg mass or laying interval in either breeding attempt (Table 4).

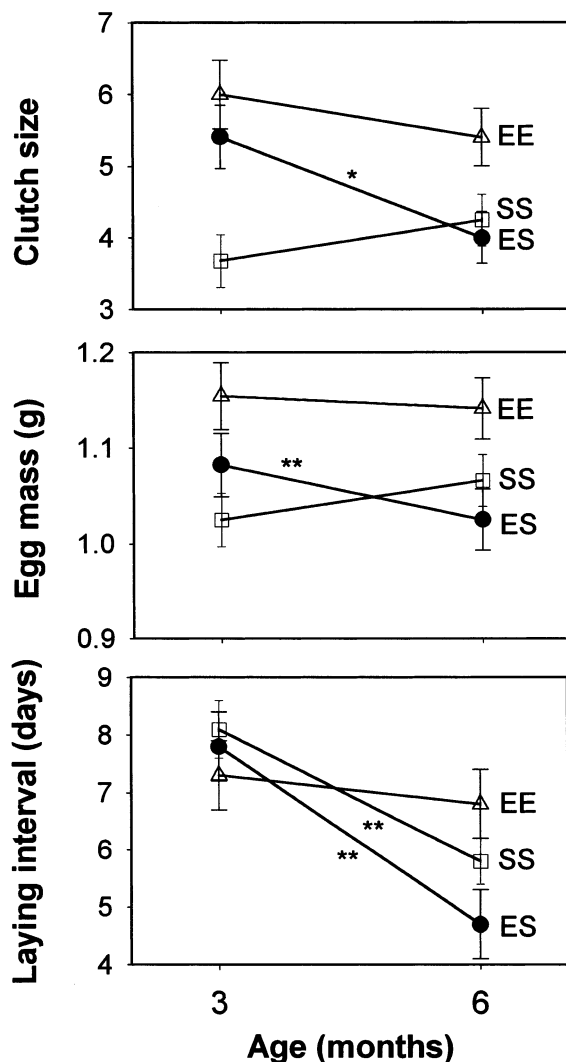


Fig. 1. Effects of age/experience and diet on clutch size, egg mass and laying interval in female zebra finches breeding at 3- and 6-months of age on a low-quality seed diet (SS; open squares) or a high-quality, egg-food supplemented diet (EE; open triangles), or at 3-months on the high-quality diet and 6-months on the low-quality diet (ES; closed circles). Asterisks indicate significant differences between the first and second breeding attempt within a treatment (* $P < 0.05$; ** $P < 0.01$).

Discussion

In this study we sought to identify true age-related variation in primary reproductive performance within-individuals (i.e. constraints) and to experimentally test whether nutritional state, manipulated through diet, affected this age-related variation. Diet quality had a significant effect on clutch size and egg mass as has been reported elsewhere (Selman and Houston 1996, Williams 1996b), but, importantly, it also influenced the effect of age on reproductive performance. Clutch size at first breeding increased with age on a low-quality diet but not on a high-quality diet, i.e., under good

conditions, young birds were able to perform as well as older birds. Clutch size was not, however, influenced by experience (i.e., for a first vs. second breeding attempt). Similarly, laying interval improved (i.e., it decreased) with age but not experience, although this effect of age, isolated from experience, was independent of diet quality. However, when age and experience were confounded (i.e., in birds that were bred at 3- and 6-months), laying interval improved with age/experience on the low-quality diet but not the high-quality diet, again indicating that the effects of age/experience may be more apparent under poorer conditions. Diet quality was actually able to completely reverse the expected age-related pattern in egg mass and clutch size: individuals that laid large clutches of large eggs at 3-months of age on the high-quality diet laid small clutches of small eggs at 6-months of age when breeding on the low-quality diet even though they were older.

To our knowledge ours is one of the few studies to date which have experimentally distinguished between the effects of age and experience on reproductive effort (see also Pärt 1995, 2001). An experimental approach offers important advantages over observational studies that attempt to disentangle the effects of age and experience statistically (e.g., by comparing individuals that 'choose' to breed for the first time at different ages) since age at first breeding is likely to covary with individual quality (Forslund and Pärt 1995). In our study since we restricted our main analyses to birds which laid both at 3- and 6-months of age, differences in individual quality among breeding attempts were unlikely to confound our results (even though there was almost certainly marked variation in individual "quality" within cohorts for each breeding attempt). Furthermore, constant conditions in captivity exclude the possibility that older birds experience better environmental conditions because they breed earlier in the season, a factor that may influence the apparent effects of age/experience in field studies. Although the physiological and behavioural factors that lead to age-related variation in clutch size and laying interval remain to be determined, our experiment has ruled out training effects specific to breeding (e.g., effects associated with the *process* of gonadal recrudescence, courtship, etc), since prior breeding experience itself did not affect reproductive performance (see also Pärt 1995). We cannot rule out the possibility that breeding experience does improve reproductive performance, but that the cost of prior breeding (at 3-months) in our experiment negated the benefits of experience. However, we think this is unlikely since females produced eggs but did not incur the costs of incubation or rearing young, and had approximately 2.5 months to recover from the costs of producing eggs in the presence of ad lib food. In addition, Williams (1996b) found no difference in mean egg mass or clutch size over three successive clutches laid over 23 days in zebra finches.

Table 3. Effects of age and breeding experience on primary reproductive effort in female zebra finches breeding on low- and high-quality diets. The effect of age was determined by comparing females breeding for the first time at 3- or 6-months of age. The effect of experience was determined by comparing females breeding for the first or second time at 6-months of age. Asterisks (*) indicate significant differences ($P < 0.05$) between ages/breeding attempts. The effect of diet was significant for all traits except laying interval in the age analyses.

Reproductive trait	Effect of age				Effect of experience			
	Low-quality diet		High-quality diet		Low-quality diet		High-quality diet	
	3-months of age	6-months of age	3-months of age	6-months of age	First breeding	Second breeding	First breeding	Second breeding
Sample size	16	13	22	9	13	28	9	10
Clutch size	3.69 ± 0.39*	5.08 ± 0.43*	5.68 ± 0.33	5.33 ± 0.52	5.08 ± 0.39	4.14 ± 0.27	5.33 ± 0.47	5.40 ± 0.44
Mean egg mass (g)	1.04 ± 0.03	1.07 ± 0.04	1.12 ± 0.03	1.15 ± 0.04	1.08 ± 0.03	1.06 ± 0.02	1.16 ± 0.04	1.15 ± 0.04
Laying interval (days)	8.13 ± 0.50*	6.38 ± 0.56*	7.59 ± 0.43*	6.89 ± 0.67*	6.38 ± 0.52	5.29 ± 0.35	6.89 ± 0.63	6.80 ± 0.59
Mass at pairing (g)	16.64 ± 0.41	18.44 ± 0.45	15.66 ± 0.35	16.97 ± 0.54	18.44 ± 0.58	16.98 ± 0.39	16.97 ± 0.69	16.90 ± 0.66

Table 4. Regression of reproductive traits and female body mass at 3- and 6-months of age on female mass at fledging ($n = 23$). These analyses control for the effect of diet; the fledging mass × diet interaction term was not significant ($P > 0.05$) and so was not included in the model.

Reproductive trait	3-months of age			6-months of age		
	slope	r ²	P	slope	r ²	P
Clutch size	-0.10 ± 0.25	0.008	0.68	0.14 ± 0.30	0.010	0.64
Mean egg mass (g)	0.03 ± 0.02	0.072	0.20	0.04 ± 0.02	0.130	0.08
Laying interval (days)	0.17 ± 0.50	0.005	0.74	-0.14 ± 0.40	0.005	0.74
Mass at pairing (g)	1.07 ± 0.38	0.255	0.01	1.05 ± 0.39	0.241	0.02

It is surprising that we did not observe effects of age on egg mass or more consistent effects on clutch size in our study species. Zebra finches are one of only a few avian species to have evolved the ability to breed in the same year they hatch (Zann 1996), and therefore if age-related variation in reproductive performance were due to physiological maturation (constraint), the effect of age should have been more pronounced in female zebra finches breeding at 3-months of age, compared with the majority of species which do not breed until ~12-months of age or older. Constant, favourable conditions in captivity may have obviated age-related increases in foraging success or competitive ability, which might drive age-dependent reproductive success in the wild (e.g. Desrochers 1992a, b, Daunt et al. 1999). However, constraint, either physiological or behavioural, is but one potential explanation for age-related changes in reproductive performance, change in optimal reproductive effort with age is a second possibility (Forslund and Pärt 1995). In zebra finches, optimal reproductive effort may change little with age, which could explain the lack of more pronounced age effects in this study. Young zebra finches would not be expected to exercise 'restraint' given that, in the wild, their first breeding attempt is likely to be their last. In free-living populations, median age of first-breeding is

92 days and the mean interval between successful clutches is 52 days, while median life expectancy is only 128 days (Zann and Runciman 1994, Zann 1996). However, if survival were related to state/condition, some individuals might have substantial residual reproductive value despite low survival in the overall population. The third possible source of age-related variation in reproductive performance, the appearance and disappearance of individuals in the breeding population (the selection hypothesis; Forslund and Pärt 1995), was ruled as a confounding factor for most of our results because we followed the same individuals at different ages. However, birds that failed to breed when first paired at 3-months of age only laid smaller eggs, but did not have different clutch size or laying interval, compared with birds that did breed at 3-months.

The question remains as to what does cause the marked variation in reproductive performance observed among individuals in egg size (0.975–1.354 g) and clutch size (3–8 eggs; see also Williams 1996a), variation that is similar in magnitude to that reported for free-living zebra finches (Zann 1996). Previous studies have suggested that environmental conditions during nestling growth can be an important determinant of clutch size (Haywood and Perrins 1992, Hōrak 1994) and egg size (Potti 1999), and this effect should be

particularly marked in zebra finches due to their short pre-reproductive lifespan. In a study on zebra finches, Haywood and Perrins (1992) reported a positive, and surprisingly strong ($r = 0.795$), correlation between clutch size and female mass at 45 days post-hatching, however, this analysis was based on 11 daughters from only four families and relatedness was not controlled for. Although all chicks were reared under constant conditions in our study there was marked individual variation in fledging mass (9.1–13.8 g), and fledging mass was a good predictor of adult breeding mass (as in many other studies, e.g. Boag 1987, Potti 1999). However, despite this we found no relationship between reproductive performance and body mass at fledging, an index of conditions during early growth. We therefore suggest that the effect of nestling growth on subsequent reproductive performance currently remains unresolved, especially for clutch size.

In conclusion, in our study nutritional condition (diet) emerged as a central component of state that could influence and in some cases even reverse any age-dependent increase in traits comprising primary reproductive effort (timing of breeding and egg-laying). These results suggest that age-dependent foraging success or access to high-quality territories might be mechanisms underlying the age-specific patterns of reproduction that are frequently observed in wild populations (Pärt 2001, Christians 2002).

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