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Egg production in oviparous vertebrates is assumed to be costly but the physiological basis of any costs remains unknown. The avian oviduct is a highly differentiated linear organ, with Þve functionally speciÞc regions. Here we show that the oviduct regresses rapidly Ôfrom the top downÕ as soon as the more proximal regions have completed their function but while the distal regions still retain an oviductal egg. In zebra Þnches *Taeniopygia guttata*, oviduct mass did not differ between early laying birds at the 1-egg stage compared with late-laying birds (with one remaining yolky follicle; dry mass, 151Ð167 mg). However, in birds with no remaining yolky follicles but with an oviductal egg, oviduct mass decreased to 84 mg (44%). Regression occurred unequally among different regions of the oviduct, with signiÞcant decreases in the proximal infundibulum/magnum and isthmus regions (59% and 40%, respectively), but no change in distal shell gland/vagina mass. The shell gland did not regress until after the last oviposition. Thus, the avian oviduct has a highly regulated sizeÐfunction relationship consistent with a high maintenance energy cost for this organ. We suggest that oviduct function is a signiÞcant contributor to the physiological costs of egg production and might med tp

Egg production in birds is widely assumed to be energetically costly (e.g. Stevenson and Bryant, 2000; Nager et al., 2000; Nilsson and Raberg, 2001; Visser and Lessells, 2001) but currently little is known about the speciÞc processes, or components of the reproductive axis, which form the physiological basis for these costs (Carey, 1996; Monaghan and Nager, 1997; Nilsson and Raberg, 2001; V zina and Williams, 2002). Most studies to date have focussed on ovarian processes in relation to differential patterns of female reproductive effort, e.g. follicle development, yolk precursor synthesis and uptake (Challenger et al., 2001; Christians and Williams, 2001), or transfer of steroid hormones from mother to offspring via yolk (e.g. Schwabl, 1993, 1996; Muller et al., 2002). In contrast, the relative importance of extra-ovarian components of the female reproductive system have rarely been considered in relation to parent—offspring interactions or in mediating variation in maternal effects (however, see Saino et al., 2001, 2002).

Recent studies have suggested that the oviduct might have high energy costs for growth and/or maintenance, contributing substantially to the energetic cost of reproduction. For example, in breeding European starlings *Sturnus vulgaris*, egg production was associated with a 22% increase in resting metabolic rate (RMR; V zina and Williams, 2002; see also Nilsson and Raberg, 2001), and oviduct mass was the only organ that explained variation in RMR among laying females (V zina and Williams, 2003). Similarly, in house sparrows *Passer domesticus*, Chappell et al. (1999) found that basal metabolic rate (BMR) was positively correlated with combined dry ovary and oviduct mass. While these studies suggest potential ÔcostsÕ to individuals with large oviducts, Christians and Williams (1999) reported a positive relationship between albumen protein content of eggs and oviduct mass, i.e. individuals with larger oviducts might beneÞt in being able to produce higher quality eggs (Williams, 1994). Given these identiÞable costs and beneÞts, this predicts that oviduct size should be tightly coupled to the functional demands of this organ (*sensu* Diamond and Hammond, 1992). In support of this idea, V zina and Williams (2003) found that total oviduct mass decreased by 47% immediately following ovulation of the last ovarian follicle even though an oviductal egg was still present at this point (though they did not identify which component(s) of the oviduct accounted for this decrease in mass).

Guillette, 1988). In poultry, an egg takes approx. 25 h to pass down the entire length of the oviduct, but spends most time

(approx. 20 h) in the distal shell gland and relatively little time in the proximal magnum and isthmus regions where albumen and shell membrane formation occur (Solomon, 1983; Bakst, 1998). Here, in zebra finches *Taeniopygia guttata*, we demonstrate that the oviduct does have a highly regulated size—function relationship. Specifically, this linear organ regresses very rapidly at the end of egg-laying from the top down as soon as the more proximal regions have completed their function but while the distal regions are still functional. This would minimize the time that the different components of this organ are maintained in a functional state, and thus reduce the energy cost of maintaining the complete oviduct.

Materials and methods

had data from two birds on the LQD with an oviductal egg and no remaining yolky follicles, but oviduct masses in these birds (73 mg, 112 mg) were similar to those in birds on the HQD at this stage (mean 91 mg, range 75—127 mg, N=15).

Total dry oviduct mass varied with stage of ovarian development ($F_{5,54}$=31.9, $P<0.001$, controlling for body mass; Fig. 1). Oviduct mass did not differ between birds at the 1-egg stage (with a full follicle hierarchy) and late-laying birds that had ovulated 3—5 follicles and had only one yolky follicle remaining (153–8 vs. 167–7 mg; $P>0.90$). However, oviduct mass then decreased by 44%, to 94–6 mg in birds with no remaining yolky follicles but still with an oviductal egg ($P<0.001$), and then decreased further to 55–10 mg in birds with no oviductal egg, i.e. in birds at clutch completion ($P<0.01$).

This reduction in oviduct dry mass over the cycle of ovarian development occurred unequally among the different regions of the oviduct (Fig. 2). The mass of the proximal infundibulum/magnum regions and the isthmus region decreased by 56% and 38%, respectively, when birds with one yolky follicle were compared with those with no yolky follicles and only an oviductal egg (Fig. 2A,B; $P<0.001$ in both cases). In contrast, there was no change in mass of the shell gland/vagina at this stage (paired contrast, $P>0.90$). Rather, shell gland/vagina mass only decreased (by 34%) 24 h later, after the last egg had been laid, i.e. in birds at clutch completion with no oviductal egg (Fig. 2C; $P<0.001$). Thus, regression of the oviduct was initiated first, and occurred most rapidly, in the proximal regions of the organ, but was delayed in the distal section until after the last oviposition. As a consequence, the relative morphology of this organ changed with stage of ovarian development. As laying progressed the relative contribution of the infundibulum/magnum regions decreased from 66.6–7.1% of total oviduct mass at the 1-egg stage to 52.5–3.6% in birds that had completed their last ovulation but still retained an oviductal egg. Conversely, the relative contribution of the shell gland/vagina regions increased from 21.7–4.5% to 34.2–2.9%, respectively.

First-laid eggs were significantly lighter than last-laid eggs for females laying ≥

sections of the oviduct even before the final oviposition. In the ~24 h period after the last follicle was ovulated, but before this egg was laid, the proximal infundibulum/magnum and the isthmus regions decreased by 56% and 38%, respectively. Over the same period there was no change in shell gland/vagina mass, but these sections regressed by 34% in mass in the ~24 h after the last oviposition. This maintenance of the functional capacity of the oviduct until last oviposition is supported by the fact that there was no decrease in absolute or relative mass of oviduct-dependent egg components (shell and albumen) for later-laid eggs.

The pattern of oviduct regression in our study is very different from that reported by Houston et al. (1995), also for the zebra finch. They suggested that the oviduct reached peak mass at the 1-egg stage but then declined in mass linearly through laying, decreasing from 120 mg to 40 mg (66%) between the 1- and 4-egg stages. Houston et al. (1995) argued that this reflected "release" of protein from the oviduct for egg formation, i.e. that the oviduct acts as a storage organ. We disagree with this conclusion and suggest that the result of Houston et al. (1995) was an artifact of (1) plotting oviduct mass by egg number (laying sequence), rather than the actual stage of ovarian development, (2) including birds at later stages of egg-laying that had actually completed egg formation, and (3) not using mass-corrected oviduct mass. Indeed, if we analyze our data this way, not accounting for these confounding factors, we also find an apparent decrease in oviduct mass between the 1- and 4-egg stage (data not shown). Although birds in the study by Houston et al. (1995) were maintained on a low-quality seed diet (in contrast to our study), our data show that diet *per se* does not explain the difference in oviduct mass between studies. Even on a seed-only diet in our study, birds late in laying had oviducts averaging 151 mg, which is much larger than the mean of 30—50 mg reported by Houston et al. (1995). Thus, we believe there is currently no evidence to support a protein storage function for the avian oviduct in relation to egg production (cf. Houston et al., 1995; see also V zina and Williams, 2003).

The results of our study clearly show that total oviduct mass remains constant during egg-laying as long as there is at least one remaining yolky follicle still to be ovulated and to pass down the oviduct. However, once the last ovulation has occurred there is rapid, and marked, regression of the proximal regions of the oviduct (the infundibulum, magnum and isthmus) as soon as the follicle has passed these regions (within 24 h post-ovulation), but while the distal shell gland region is still processing the oviductal egg. Part of this decrease might be explained by loss of stored secretory products (albumen proteins) from oviductal tissue following the last ovulation. This does not fully explain the differential pattern of oviduct regression we report, but this source of mass loss would still be consistent with rapid downregulation of oviduct function (although in the domestic hen, albumen protein content of the magnum region does not decrease until after cessation of laying; Yu and Marquardt, 1973). Our result is very similar to that reported for laying female European starlings, where oviduct mass also remains constant up to the last ovulation, but then decreases by 50% following this last ovulation in birds with only one oviductal egg remaining (V zina and Williams, 2003). Thus, in two small passerines, the avian oviduct has a highly regulated

1st egg | > F1 foll + ovid egg | F1 foll + ovid egg | 0 foll + ovid egg | 0 foll No ovid egg

Stage of ovarian development

egg2 l /F30 11TD76oF744.49 Tf7 158D ( )T5 0f 1 Tf 3.41 0 g7 1 1 0gg

size—function relationship consistent with a high energy cost of maintenance for this organ (i.e. high levels of cellular secretory activity). This interpretation is supported by the observation that individual variation in residual RMR in European starlings during egg-laying is positively related to oviduct mass but not to other organs (V zina and Williams, 2003). There appears to be little known about the specific mechanisms involved in oviduct regression, but our study suggests that these mechanisms must be specific to each region of the oviduct (e.g. differential timing of receptor expression) rather than involving a more generic, humoral signal such as downregulation of plasma estrogen or progesterone levels (Burley and Vadehra, 1989). Although we did not investigate the growth phase, Yu and Marquardt (1973) showed that the rate of growth of the magnum during oviduct development is much greater than that of more distal sections of the oviduct, i.e. the pattern of growth also closely reflects functional demands.

Although maintenance of a large oviduct would appear to be costly, there are likely advantages to having a large oviduct in terms of both the quantity, and potentially the quality, of egg albumen. Albumen protein content of eggs is positively related to oviduct mass (Christians and Williams, 1999), and this might be important for offspring fitness in terms of structural growth of the offspring (Williams, 1994; Finkler et al., 1998). In addition, several recent studies have suggested that maternal effects might include transfer of immunoglobulins and antibacterial factors from mother to offspring in egg albumen (Saino et al., 2001, 2002); thus, oviduct size/function might play a role in mediating these maternal effects. Nevertheless, we consider it unlikely that oviduct size determines egg size, via albumen content, independently of ovarian factors that determine yolk size (Williams et al., 2001). Rather, it seems more likely that high quality birds which produce large yolks must also be able to sustain the high costs of oviduct function to deposit the appropriate amount of albumen required by yolks of a particular size. It is clear that animals possess considerable phenotypic flexibility in body composition, undergoing reversible changes in organ size, e.g. in relation to migration (Battley et al., 2000; Guglielmo and Williams, 2003) or reproduction (V zina and Willams, 2003). However, in general these studies have focussed on modulation at the whole-organ level. We suggest that the type of intra-organ structure—function relationship documented here for the avian oviduct might also occur in other linear organs with high maintenance energy costs where there is temporal separation of function, e.g. in digestive tracts with prolonged passage times (Secor and Diamond, 1997).

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