Behavioral and physiological flexibility are used by birds to manage energy and support investment in the early stages of reproduction

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Abstract   Interest in phenotypic flexibility has increased dramatically over the last decade, but flexibility during reproduction has received relatively little attention from avian scientists, despite its possible impact on fitness. Because most avian species maintain atrophied reproductive organs when not active, reproduction in birds requires major tissue remodeling in preparation for breeding. Females undergo rapid (days) recrudescence and regression of their reproductive organs at each breeding attempt, while males grow their organs ahead of time at a much slower rate (weeks) and may maintain them at maximal size throughout the breeding season. Reproduction is associated with significant metabolic costs. Egg production leads to a 22%–27% increase in resting metabolic rate (RMR) over non-reproductive values. This is partly due to the activity of the oviduct, an organ that may allow females to adjust reproductive investment by modulating egg size and quality. In males, gonadal recrudescence may lead to a 30% increase in RMR, but the data are inconsistent and general conclusions regarding energetic costs of reproduction in males will require more research. Recent studies on captive female zebra finches describe the impacts of these costs on daily energy budgets and highlight the strategies used by birds to maintain their investment in reproduction when energy is limited. Whenever possible, birds use behavioral flexibility as a first means of saving energy. Decreasing locomotor activity saves energy during challenges such as egg production or exposure to cold temperatures and is an efficient way to buffer variation in individual daily energy budgets. However, when behavioral flexibility is not possible, birds must rely on flexibility at the physiological level to meet energy demands. In zebra finches breeding in the cold, this results in a reduced pace of laying, likely due to down-regulation of both reproductive and non-reproductive function, allowing females to defend minimal egg size and maintain reproductive success. More research involving a range of species in captive and free-living conditions is needed to determine how phenotypic flexibility during tissue remodeling and early reproductive investment translates to natural conditions and affects fitness [*Current Zoology* 56 (6): 767–792, 2010].

Key words   Phenotypic plasticity, Phenotypic flexibility, BMR, Energy budget, Organ, Egg size, Physiological tradeoff, Fitness

1   Introduction

Phenotypic flexibility is defined as the capacity for an individual organism to reversibly transform its phenotype (Piersma and Drent, 2003). It is one of four sub-categories of phenotypic plasticity that also include developmental plasticity, polyphenism and life-cycle staging (Piersma and Drent, 2003). Over the last two decades, evolutionary biologists have shown a growing interest in phenotypic flexibility. A search on Web of Science for papers specifically using the term "phenotypic flexibility" in their title, abstract or key words shows a clear trend for an increasing number of publications per year referring to the phenomenon (Fig. 1), with numbers taking off in years following Piersma and

Drent's (2003) conceptual distinction of flexibility within plasticity. Although confusion remains with the use of the broader term phenotypic plasticity, this simple survey clearly shows that interest in phenotypic flexibility is growing in the collective scientific mind.

Although all spheres of evolutionary biology may now include studies on adaptive phenotypic flexibility, avian research has been particularly active over the last decade. Indeed, of all papers published since 1990 that were reported by Web of Science as using the term phenotypic flexibility, 43% (71 of 167 papers) were based on or involved avian systems (using key word "bird*"). There are many examples of phenotypic flexibility in birds (e.g. Piersma and Lindstom, 1997; Starck, 2005; McKechnie, 2008; Swanson, 2010) but some
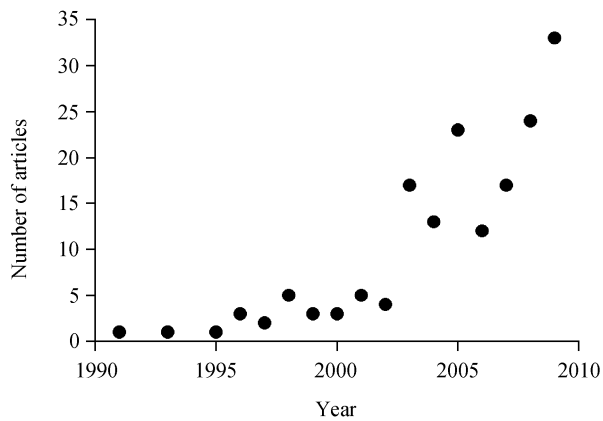
Fig. 1   Number of articles using the term "phenotypic flexibility" in their title, abstract or keywords since 1990 according to Web of Science

The search used the Science Citation Index Expanded Database and excluded year 2010.

aspects of their life history have received more attention than others. For example, long distance migration is generally recognized as a highly demanding activity involving considerable flexibility in several physiological traits, from endocrine adjustments (e.g. Holberton, 1999, Piersma et al., 2000; Landys-Ciannelli et al., 2002; Landys et al., 2004) to changes in nutrient transport and fuel use (McWilliams et al., 2004, Weber, 2009, Swanson, 2010), organ size (e.g. Piersma et al., 1996, Biebach, 1998, Battley et al., 2000, Piersma, 2002; Guglielmo and Williams, 2003; Bauchinger et al., 2005) and metabolic performance (Swanson and Dean, 1999; Battley et al., 2001, Kvist and Lindstrom, 2001; McKechnie, 2008). Birds have also been shown to exhibit remarkable flexibility at several levels of integration when faced with specific food types requiring reversible adjustments in their digestive machinery (Piersma et al., 1993; Piersma et al., 1999; Starck, 1999; Dekinga et al., 2001; Battley and Piersma, 2005). Flexibility in metabolic performance (measured as basal metabolic rate; BMR, and maximal thermogenic capacity; M_{sum}), evaporative water loss and skin structure, as well as in the size of internal organs have also been highlighted in the context of seasonal acclimatization and laboratory acclimation to different temperatures (Williams and Tieleman, 2000; Haugen et al., 2003; Tieleman et al., 200; McKechnie et al., 2007; Cavieres and Sabat, 2008; McKechnie, 2008; Zheng et al., 2008, Barcelo et al., 2009; Swanson, 2010). In this specific case, although the majority of studies have focused on non-migratory bird species from northern latitudes (Smit and McKechnie, 2010), new evidence from studies including migratory species or species experiencing

seasonally stable, relatively mild or dry environments support the hypothesis that phenotypic flexibility in response to thermal regime is a common feature of birds (Williams and Tieleman, 2000; Tieleman et al., 2003; Klaassen et al., 2004; McKechnie et al., 2007; Cavieres and Sabat, 2008; Barcelo et al., 2009; Maldonado et al., 2009; Salvante et al., 2010). With the realization that a wide variety of phenotypic traits in animals are flexible (Piersma and Drent, 2003), scientists are now interested in testing the adaptive value of phenotypic flexibility by linking flexibility with fitness (e.g. Ricklefs and Wikelski, 2002; Seebacher, 2005; Naya et al., 2008; Moore and Hopkins, 2009).

A surprising fact associated with the growing interest in phenotypic flexibility is that perhaps one of the best-known examples of avian physiological flexibility appears to have attracted very little attention. According to Web of Science, of the 71 papers on avian systems published since 1990 which use the term "phenotypic flexibility", only one (1.4%) explicitly studied flexibility in reproductive traits (Partecke et al., 2004). However, this rough survey misses studies wrongly referring to plasticity instead of flexibility. The same analysis using the term "phenotypic plasticity" shows that only 35% of studies investigated aspects of reproduction. Yet, reproduction in birds is associated with major phenotypic changes at multiple levels, from endocrine induction to internal organ reorganization leading to new tissue synthesis (e.g., reproductive organ growth, egg production) (Opel and Nalbanov, 1961a, b;Yu et al., 1971; Follett and Maung, 1978; Dawson and Goldsmith, 1983; Burley and Vadehra, 1989; Etches, 1996; Williams, 1998; Vézina and Williams, 2003). These transformations have measurable energetic costs (Chappell et al., 1999; Nilsson and Raberg, 2001; Vézina and Williams, 2002, 2005a; Salvante et al., 2010), and these costs may result in reversible changes in behavior and physiology with consequences for energy budgets (Houston et al., 1995; Williams and Ternan, 1999; Vézina and Williams, 2005b; Vézina et al., 2006; Salvante et al., 2007, 2010; Williams et al., 2009). The scarcity of avian studies on phenotypic flexibility during reproduction is even more surprising given that phenotypic changes associated with variation in individual reproductive investment may presumably be directly linked with reproductive success (e.g. oviduct size vs egg size and quality, Ricklefs 1976, Christians and Williams 2001a, Vézina and Williams 2003), a major component of fitness.

Physiological reproductive effort (i.e. egg production)

has also been linked to adult survival, the second component of fitness. Indeed manipulative experiments have shown negative effects of experimentally increased reproductive effort on reappearance of adult females the following years (Heaney and Monaghan, 1995; Nager et al., 2001; Visser and Lessells, 2001; Nager, 2006). These effects are likely mediated by long-term consequences on physiological condition (reviewed by Nager, 2006). Similar findings in natural populations experiencing mismatches between the timing of reproduction and the natural peak of food resources also suggest a survival cost to reproductive effort (e.g. Thomas et al., 2001).

With this overview, our aim is to highlight current information on avian reproductive phenotypic flexibility in the context of energy management strategies. We suggest new research avenues that are likely to help in understanding how flexibility may influence reproductive success by allowing breeding birds to balance their energy budgets. The notion that reproduction is a highly energy-demanding life-history stage in birds has been formulated from decades of studies on avian reproduction (e.g. Drent and Daan, 1980) which, for the most part, have focused on the periods of incubation or, in altricial species, nestling provisioning (Williams and Vézina, 2001; Williams, 2005; Nager, 2006). These life-history stages certainly deserve our attention in the context of adaptive phenotypic flexibility and fitness. However this paper will focus on the much less studied period of reproductive organ recrudescence, egg formation and laying.

2 Seasonal Remodeling of Body Composition

Timing reproductive effort to coincide with resource availability in a seasonal environment is crucial for birds as it may significantly contribute to reproductive success and fitness. Reproduction in birds is generally timed to match the peak of nestling demand with maximal food abundance or the seasonal availability of specific dietary resources (Perrins, 1996; Williams, 1998). However, the vast majority of avian species maintain their reproductive organs in an atrophied state throughout all non-reproductive stages (Williams, 1998). Consequently, gonadal recrudescence, egg formation and fertilization, egg laying and incubation, which all occur prior to the period of nestling care, generally happen at a time when environmental conditions may be suboptimal in terms of nutrient and energy availability (Perrins, 1996). Yet major reversible organ changes occur in both

sexes in preparation for breeding. With global climate change, mismatches in timing of breeding and food resource availability (e.g. Visser et al., 2006) are likely to exacerbate this situation and further reduce energy availability for pre-breeding body remodeling.

In females, reported changes in oviduct size from a non-breeding to a reproductively mature state can range between 5- to 220-fold, while ovarian development can lead to a mature organ that is 4- to 75-fold larger than the immature state (Table 1). In males, testicular growth exhibits a larger magnitude of increase, with mature testes growing up to 480-fold larger than their non-reproductive size (Table 2). However, mature reproductive organs of females typically represent a larger proportion of total body mass compared to those of males (average 8.6% and 1.5% of non-reproductive body mass in females and males, respectively, considering only wet mass data and natural conditions from Tables 1 and 2).

In females of species where the pattern of organ recrudescence has been detailed, growth of reproductive organs happens in synchrony with rapid yolk development, preceding the ovulation of the first ovarian follicle. This period can be very rapid in small species (4 days in the opportunistic breeding zebra finch *Taenyopigia guttata*, 6 days in the seasonal breeding European starling, *Sturnus vulgaris*) and may take up to 25 days in larger species like the Pacific black brant *Branta bernicla nigricans* (Table 1). In males, however, gonadal recrudescence is a much slower process that can take 2–8 weeks to complete under natural conditions (Table 2), often beginning as early as during the winter season (e.g. Hegner and Wingfield, 1986c; Wikelski et al., 2003; Raes and Gwinner, 2005; Caro et al., 2006).

Even though several bird species lay more than one clutch per season, recent evidence in passerines strongly suggests that individual females go through cycles of recrudescence and regression of their reproductive organs at each reproductive attempt in order to minimize the energetic costs associated with maintaining and carrying these organs (Vézina and Williams, 2003; Williams and Ames, 2004). In contrast, males can maintain their mature testes for much longer (Table 2), up to six months in rufous-winged sparrows *Aimophila carpalis* (Small et al., 2007). However, the pattern of recrudescence and regression may differ significantly among species and breeding strategies. For instance, female house sparrows *Passer domesticus* produce several clutches of eggs per breeding season and male testes remain fully developed for the entire breeding season

Table 1 Gonadal development in female birds

Species	Reproductive organ/tissue	ANRBM	NRSO	RSO	XIS	RRM	MDG	MDM	Measurement conditions	References
Pacific black brant	†Ovary mass (g)*	1431*	0.4	2.15	5.375	0.15	< 25 days		Natural	Mason et al., 2007
Branta bernicla nigricans										
Mallard duck	Oviduct mass (g) W	967.3*	7.2	32.1	4.5	3.32			Natural	Krapu, 1981
Anas platyrhynchos	Ovary mass (g) W		1.8	31.9	17.7	3.30			Natural	Krapu, 1981
Ruddy duck	Oviduct mass (g) D	529	0.9	7.7	8.6	1.46			Natural	Tome, 1984; mass: Hohman et al., 1992
Oxyura jamaicensis	Ovary mass (g) D		0.2	15.04	75.2	0.28			Natural	Tome, 1984; mass: Hohman et al., 1992
European barn owl	Ovary mass (mg)*	305.8	30.9	182.0	5.9	0.06			Carcass measurements of birds with fat score >1	Young et al., 2009; mass: Massemin et al., 1997
Tyto alba	Ovary mass (mg)*		39.8	199.5	5.0	0.07			Carcass measurements of adult birds	Young et al., 2009; mass: Massemin et al., 1997
	Ovary mass (mg)*		25.1	398.1	15.8	0.13			Carcass measurements of first year birds	Young et al., 2009; mass: Massemin et al., 1997
European sparrowhawk	Ovary mass (mg)*	260*	15.1	186.2	12.3	0.07			Carcass measurements of birds with fat score >1	Young et al., 2009; mass: Vedder et al., 2005
Accipiter nisus	Ovary mass (mg)*		31.6	251.2	7.9	0.10			Carcass measurements of adult birds	Young et al., 2009; mass: Vedder et al., 2005
	Ovary mass (mg)*		13.8	177.8	12.9	0.07			Carcass measurements of first year birds	Young et al., 2009; mass: Vedder et al., 2005
Kestrel	Ovary mass (mg)*	217	31.6	316.2	10.0	0.15			Carcass measurements of birds with fat score >1	Young et al., 2009; mass: Jonsson et al., 1996
Falco tinnunculus	Ovary mass (mg)*		39.8	316.2	7.9	0.15			Carcass measurements of adult birds	Young et al., 2009; mass: Jonsson et al., 1996
	Ovary mass (mg)*		12.6	158.5	12.6	0.07			Carcass measurements of first year birds	Young et al., 2009; mass: Jonsson et al., 1996
European starling	Oviduct mass (g) LD	77	0.014	0.965	68.9	1.25	6 days		Natural	Vézina unpublished data

Table 1 (*Continued*)

Species	Reproductive organ/tissue	ANRBM	NRSO	RS	XIS	RRM	MDG	MDM	Measurement conditions	References
Sturnus vulgaris	Ovary mass (g) LD		0.01	0.05	5.0	0.06	6 days		Natural	Vézina unpublished data
	Ovarian follicle mass (g) LD		0.01	0.28	28.0	0.36	6 days		Natural	Vézina unpublished data
	Oviduct mass (g) W		0.08	3.99	49.9	5.18	6 days		Natural	Vézina unpublished data
	Ovary mass (g) W		0.07	0.27	3.9	0.35	6 days		Natural	Vézina unpublished data
	Ovarian follicle mass (g) W		0.01	1.19	119.0	1.55	6 days		Natural	Vézina unpublished data
Clay-colored robin *Turdus grayii*	Largest ovarian follicle diameter (mm)*	67.9*	0.5	4.7	9.4				Natural	Wikelski et al., 2003
Blue-gray tanager *Thraupis episcopus*	Largest ovarian follicle diameter (mm)*	32.8*	0.5	3.7	7.4				Natural	Wikelski et al., 2003
Bicolored antbird *Gymnopithys leucaspis bicolor*	Largest ovarian follicle diameter (mm)*	29.4*	0.5	3.1	6.2				Natural	Wikelski et al., 2003
House sparrow *Passer domesticus*	Oviduct mass (mg) D	28.4	0.006	0.333	55.5	1.17				Krementz and Ankney, 1986; mass: Johnston and Selander, 1973
House sparrow *Passer domesticus*	Largest ovarian follicle diameter (mm)*	27.5*	0.1	6	60			<3 weeks	Natural	Hegner and Wingfield, 1986b
Pacific black brant *Branta bernicla nigricans*	†Ovary mass (g)*	1431*	0.4	2.15	5.375	0.15	< 25 days		Natural	Mason et al., 2007
Mallard duck	Oviduct mass (g) W	967.3*	7.2	32.1	4.5	3.32			Natural	Krapu, 1981

Species	Reproductive organ/tissue	ANRBM	NRSO	RS	XIS	RRM	MDG	MDM	Measurement conditions	References
Anas platyrhynchos	Ovary mass (g) W		1.8	31.9	17.7	3.30			Natural	Krapu, 1981
Ruddy duck	Oviduct mass (g) D	529	0.9	7.7	8.6	1.46			Natural	Tome, 1984; mass: Hohman et al., 1992
Oxyura jamaicensis	Ovary mass (g) D		0.2	15.04	75.2	0.28			Natural	Tome 1984; mass: Hohman et al. 1992
European barn owl	Ovary mass (mg)*	305.8	30.9	182.0	5.9	0.06			Carcass measurements of birds with fat score >1	Young et al., 2009; mass: Massemin et al., 1997
Tyto alba	Ovary mass (mg)*		39.8	199.5	5.0	0.07			Carcass measurements of adult birds	Young et al., 2009; mass: Massemin et al., 1997
	Ovary mass (mg)*		25.1	398.1	15.8	0.13			Carcass measurements of first year birds	Young et al., 2009; mass: Massemin et al., 1997
European sparrowhawk	Ovary mass (mg)*	260*	15.1	186.2	12.3	0.07			Carcass measurements of birds with fat score >1	Young et al., 2009; mass: Vedder et al., 2005
Accipiter nisus	Ovary mass (mg)*		31.6	251.2	7.9	0.10			Carcass measurements of adult birds	Young et al., 2009; mass: Vedder et al., 2005
Song wren	Largest ovarian follicle diameter (mm)*	23*	0.5	2.3	4.6				Natural	Wikelski et al., 2003
Cyphorhinus phaeocephalus										
White-crowned sparrow	Ovary mass (mg) W F	23	4.9	18.6	3.8	0.08			Natural: Spring migration	Farner et al., 1966
Zonotrichia leucophrys gambelii	Ovary mass (mg) W F		4.9	326	66.5	1.42			Natural: Breeding maximum	Farner et al., 1966
	Ovarian follicle diameter (mm)*		0.5	> 5	at least 10				Natural: Categorized: non-breeding <0.5 mm, reproductive >5 mm	Wingfield and Farner, 1978a
Zonotrichia leucophrys pugetensis	Ovarian follicle diameter (mm)*	24.5*	0.5	> 5	at least 10		~1 week	~7 days	Natural: Categorized: non-breeding <0.5 mm, reproductive >5 mm	Wingfield Farner, 1978b

Table 1 (*Continued*)

Species	Reproductive organ/tissue	ANRBM	NRSO	RS	XIS	RRM	MDG	MDM	Measurement conditions	References
Great tit	Oviduct mass (mg)* W F	18.34	1	220	220	1.20			Natural	Silverin, 1978; mass: Broggi et al., 2007
Parus major	Ovary mass (mg)* W F		1	65	65	0.35			Natural	Silverin, 1978; mass: Broggi et al., 2007
Zebra finch	Oviduct mass (mg) LD	17	5.97	120	20.1	0.71	4 days	< 10 days	Natural: Captive	Houston et al., 1995
Taeniopygia guttata										
Spotted antibird	Largest ovarian follicle diameter (mm)*	16.9*	0.5	7.5	15				Natural	Wikelski et al., 2003
Hylophylax n. naevioides										
Golden-collared manakin	Largest ovarian follicle diameter (mm)*	15.5*	0.5	4.7	9.4				Natural	Wikelski et al., 2003
Manacus vitelinus										
Red-capped manakin	Largest ovarian follicle diameter (mm)*	13.8*	0.5	6	12				Natural	Wikelski et al., 2003
Pipra mentalis										
Pied Flycatcher	Oviduct mass (g) LD	12.30*	0.04	0.24	6	1.95			Natural	Ojanen, 1983b
Ficedula hypoleuca	Ovary mass (g) LD		0.01	0.12	12	0.98			Natural	Ojanen, 1983b
	Oviduct mass (g) W		0.18	1.00	5.6	8.13			Natural	Ojanen, 1983b
	Ovary mass (g) W		0.04	0.67	16.75	5.45			Natural	Ojanen, 1983b
Williow tit	Largest ovarian follicle diameter (mm)*	10.94	0.25	0.96	3.84				Experimental (may not be fully developed)	Silverin and Westin, 1995; mass: Broggi et al., 2003
Parus montanus										

† All ovary masses do not include the mass of the ovarian follicles. * Approximated from figure.

D: Dry.　F: Fixed.　LD: Lean dry.　W: Wet.

ANRBM: Average non-reproductive body mass (g). MDG: Minimum duration of organ/tissue growth. MDM: Minimum duration of maintenance of fully-developed organ/tissue. NRSO: Non-reproductive size of organ/tissue. RRM: Relative reproductive organ/tissue mass (compared to non-reproductive body mass) (%). RSO: Reproductive size of organ/tissue. XIS: X-fold increase in organ/tissue size relative to its non-reproductive size.

Table 2   Gonadal development in male birds

Species	Reproductive organ/tissue	ANRBM	NRSO	RSO	XIS	RRM	MDG	MDM	Measurement conditions	References
Pacific black brant	Combined testes mass (g)*	1610*	0.4	2.4	6.0	0.15	< 40 days		Natural	Mason et al., 2007
Branta bernicla nigricans										
European barn owl	Combined testes mass (mg)*	286.9	32.4	295.8	9.1	0.10		few months	Carcass measurements of birds with fat score >1	Young et al., 2009; mass: Massemin et al., 1997
Tyto alba	Combined testes mass (mg)*		41.8	490.9	11.7	0.17		few months	Carcass measurements of adult birds	Young et al. 2009, mass: Massemin et al., 1997
	Combined testes mass (mg)*		32.4	257.6	7.9	0.09		few months	Carcass measurements of first year birds	Young et al., 2009; mass: Massemin et al., 1997
Black-billed magpie	Combined testes mass (mg)	186.5	4	1250	312.5	0.67	~3 months		Natural	Erpino, 1969; Mass: Trost, 1999
Pica pica										
Kestrel	Combined testes mass (mg)*	185	10.5	224.4	21.4	0.12		few months	Carcass measurements of birds with fat score >1	Young et al., 2009; mass: Jonsson et al., 1996
Falco tinnunculus	Combined testes mass (mg)*		21.4	229.6	10.7	0.12		few months	Carcass measurements of adult birds	Young et al., 2009; mass: Jonsson et al. 1996
	Combined testes mass (mg)*		6.3	126.2	20.0	0.07		few months	Carcass measurements of first year birds	Young et al., 2009; mass: Jonsson et al., 1996
European sparrowhawk	Combined testes mass (mg)*	160*	10.5	200.0	19.1	0.13		few months	Carcass measurements of birds with fat score >1	Young et al., 2009; mass: Vedder et al., 2005
Accipiter nisus	Combined testes mass (mg)*		11.5	257.6	22.4	0.16		few months	Carcass measurements of adult birds	Young et al., 2009; mass: Vedder et al., 2005
	Combined testes mass (mg)*		10.7	135.2	12.6	0.08		few months	Carcass measurements of first year birds	Young et al., 2009; mass: Vedder et al., 2005
European starling	Combined testes mass (mg)* W	81.5	4	800	200.0	0.98	4 weeks		Experimental	Dawson et al., 2002; mass: Hicks, 1934
Sturnus vulgaris										
	Combined testes mass (mg)* W		4	1750	437.5	2.15	~60 days	1.5–2 months	Natural	Ball and Ketterson, 2008; mass: Hicks, 1934
	Testis volume (mm³)*		2.5	530.0	212.0			~2 months	Experimental	Dawson, 2005; mass: Hicks, 1934
	Testis volume (mm³)*		2.5	500.0	200.0			~2 months	Natural	Dawson, 2005; mass: Hicks, 1934

(*to be continued on the next page*)

Table 2 (*Continued*)

Species	Reproductive organ/tissue	ANRBM	NRSO	RS	XIS	RRM	MDG	MDM	Measurement conditions	References
Groove-billed ani	Combined testes mass (mg) W	79	54 (mid-incubation)	380 (laying)	7.0	0.48			Natural: Alpha male = primary incubator	Vehrencamp, 1982
Crotophaga sulcirostris	Testis length (mm)		4.5 (mid-incubation)	10 (laying)	2.2				Natural: Alpha male = primary incubator	Vehrencamp, 1982
	Combined testes mass (mg) W	73.5	202 (mid-incubation)	244 (early-incubation)	1.2	0.33			Natural: Subordinate males = limited incubation behaviour	Vehrencamp, 1982
	Testis length (mm)		7.5 (mid-incubation)	9 (early-incubation)	1.2				Natural: Subordinate males = limited incubation behaviour	Vehrencamp, 1982
Clay-colored robin	Testis volume (mm^3)*	75.7*	0.5	8.7	17.4				Natural	Wikelski et al., 2003
Turdus grayii										
Brown-headed cowbird	**Estimated combined testes mass (mg)	47*	50	780	15.6	1.66	4 weeks	~6 weeks	Natural	Dufty and Wingfield, 1986
Molothrus ater										
Blue-gray tanager	Testis volume (mm^3)*	34.2*	0.5	5.3	10.6				Natural	Wikelski et al., 2003
Thraupis episcopus										
Bicolored antbird	Testis volume (mm^3)*	30.7*	1.0	7.1	7.1				Natural	Wikelski et al., 2003
Gymnopithys leucaspis bicolor										
House sparrow	**Estimated combined testes mass (mg)*	27.5*	12	1000	83.3	3.64		4 months	Natural (not sure if non-reproductive testis size is basal)	Hegner Wingfield, 1986a
Passer domesticus										
	**Estimated combined testes mass (mg)*		4	1000	250.0	3.64	~2 months		Natural	Hegner Wingfield, 1986c
White-crowned sparrows	Combined testes mass (mg) W F	25.5	2.2	95.4	43.4	0.37			Natural: Spring migration	Farner et al., 1966
Zonotrichia leucophrys gambelii	Combined testes mass (mg) W F		2.2	884.0	401.8	3.47			Natural: Breeding max	Farner et al., 1966
	**Estimated combined testes mass (mg)*	25.5	2	960	480.0	3.76	~4 weeks	~4–6 weeks	Natural	Wingfield Farner, 1978a
Zonotrichia leucophrys pugetensis	**Estimated combined testes mass (mg)*	26.5*	2	1000	500.0	3.77	~2 weeks	~3 months	Natural	Wingfield Farner, 1978b
Song wren	Testis volume (mm^3)*	25.4*	0.5	5.7	11.4				Natural	Wikelski et al., 2003
Cyphorhinus phaeocephalus										
Great tit	Testis length (mm)*	18.34	1.25	6.5–7	5.2–5.6		15–43 days		Experimental	Silverin et al., 2008; mass: Broggi et al., 2007

(*to be continued on the next page*)

Table 2   (*Continued*)

Species	Reproductive organ/tissue	ANRBM	NRSO	RS	XIS	RRM	MDG	MDM	Measurement conditions	References
Parus major										
	Testis volume (mm³)*		1.0	2.5–2.75	2.5–2.75		11 weeks		Experimental	Caro and Visser, 2009; mass: Broggi et al., 2007
	Combined testes mass (mg)* W F		2	260	130.0	1.42			Natural	Silverin, 1978; mass: Broggi et al., 2007
Golden-collared manakin	Testis volume (mm³)*	18.1*	0.5	9.3	18.6				Natural	Wikelski et al., 2003
Manacus vitelinus										
Spotted antbird	Testis volume (mm³)*	17.8*	3.5	11.3	3.2		6 weeks		Natural (not sure if non-reproductive testis size is basal)	Hau et al., 2000
Hylophylax n. naevioides										
	Testis volume (mm³)*	17*	0.5	9.6	19.2				Natural	Wikelski et al., 2003
Dark-eyed junco	Combined testes mass (mg)* W	17.6*	5	384	76.8	2.18	~5 weeks	2 months	Natural: After second year males	Deviche et al., 2000
Junco hyemalis	Combined testes mass (mg)* W		5	339	67.8	1.93	~5 weeks	2 months	Natural: Second year males	Deviche et al., 2000
	Paired testes volume (mm³)		1.2	116.2	96.8		4 months		Experimental (not sure if testes are fully developed)	Engels and Jenner, 1956
European stonechats	Testis width (mm)*	16	1	4.5	4.5				Natural (not sure if non-reproductive testis size is basal)	Raess and Gwinner, 2005; mass: Klaassen, 1995
Saxicola torquata rubicola										
Siberian stonechats	Testis width (mm)*		0.4	4.8	12				Natural	Raess and Gwinner, 2005
Saxicola torquata maura										
Rufous-winged sparrows	Testis diameter (mm)*	15.5*	1.0	4.5	4.5			6 months	Natural	Small et al., 2007
Aimophila carpalis										
Red-capped manakin	Testis volume (mm³)*	14*	0.5	8.7	17.4				Natural	Wikelski et al., 2003
Pipra mentalis										

Table 2 (*Continued*)

Species	Reproductive organ/tissue		ANRBM	NRSO	RSO	XIS	RRM	MDG	MDM	Measurement conditions	References
Pied Flycatcher	Combined testes mass (mg)*	W F	12.1	2.93	73.34	25.0	0.61			Natural	Silverin, 1975; mass: Saetre et al., 1995
Ficedula hypoleuca											
Williow tit	Testis length (mm)*		11.53	1.3	5.0	3.8		15 days		Experimental (not sure if testes are fully developed)	Silverin and Westin, 1995; mass: Broggi et al., 2003
Parus montanus											

* Approximated from figure. ** Based on comparisons with preserved specimens of known mass

D: Dry.   F: Fixed.   LD: Lean dry.   W: Wet.

ANRBM: Average non-reproductive body mass (g). MDG: Minimum duration of organ/tissue growth. MDM: Minimum duration of maintenance of fully-developed organ/tissue. NRSO: Non-reproductive size of organ/tissue. RRM: Relative reproductive organ/tissue mass (compared to non-reproductive body mass) (%). RSO: Reproductive size of organ/tissue. XIS: X-fold increase in organ/tissue size relative to its non-reproductive size.

(Hegner and Wingfield, 1986b). In single-brooded species however, males may regress their testes rapidly following a breeding attempt. This is the case in pied flycatchers *Ficedula hypoleuca* from Sweden where a sharp decline in testes mass is observed after clutch completion (Silverin, 1975). In this specific case, males are breeding once per season, and females that lose their eggs can re-lay a new clutch, but only when paired with a different male. In single-brooded populations of white-crowned sparrows *Zonotrichia leucophrys*, testes begin regressing during incubation and decline rapidly during nestling provisioning (Wingfield and Farner, 1978a), but in populations where breeding pairs produce a second brood, the testes regress only slightly (20%) during incubation and grow back during the formation of the second clutch of eggs (Wingfield and Farner, 1978b). In the groove-billed ani *Crotophaga sulcirostris*, a tropical, communally-nesting cuckoo, the pattern of testes recrudescence and regression depends on the male's social status (Vehrencamp, 1982). Dominant males are the primary incubators, and they significantly regress their testes during incubation. Meanwhile the magnitude of testes regression in subordinate males, which perform the least amount of incubation, is much less pronounced. Anis are opportunistic breeders and breed during most of the year. Maintaining large, functional testes throughout the breeding season presumably allows for multiple breeding events and extra pair copulation. However, this may be incompatible with male incubation behavior.

Non-reproductive organs have also been reported to change in association with gonadal recrudescence but the pattern of organ flexibility appears inconsistent, at least in females, among species and among years within species (Christians and Williams, 1999; Vézina and Williams, 2003; Nager, 2006). These changes will be further discussed in the sections below.

3 The Metabolic Cost of Reproductive Investment

3.1 Females

The energetic investment in egg production has now been measured empirically five times in four passerine species (Table 3). The best estimates come from comparisons of resting or basal metabolic rates (RMR and BMR, respectively) in females measured before gonad recrudescence and during active egg production (i.e. in females with fully mature reproductive organs and an egg in the oviduct). Note that the term basal metabolic rate technically refers to animals not actively involved in new tissue synthesis. Although this criterion may be met in non-reproductive birds, it is not the case in birds measured during egg production and active spermatogenesis. While some authors did not make this distinction, for clarity we use the term resting metabolic rate hereafter.

Measurements in free living great tits *Parus major*, European starlings and captive zebra finches showed that females actively producing eggs have a resting metabolic rate 22%–27% above non-reproductive RMR values. Estimates are consistent for the three species whether measurements were performed within or among individuals (Table 3), and this cost has been shown to be repeatable in zebra finches (Vézina and Williams, 2005a). The cost of reproductive investment in females has also been measured in house sparrows using a different approach (Chappell et al., 1999). All birds were measured during the reproductive period and, although

Table 3   Energy cost of egg production in species for which measurements have been made by comparing resting or basal metabolic rates of females before gonad recrudescence and during active egg production

Species	Reference stage	Breeding stage	% increase in RMR[5]	Comparison type	Reference
House sparrow *Passer domesticus*	Non breeding[1]	Large gonads[3]	16	Among individuals	Chappell et al.,1999
Great tit *Parus major*	Wintering	1–6 eggs laid	(27)	Among individuals	Nilsson and Raberg, 2001
European starling *Sturnus vulgaris*	Non breeding[2]	Six yolky follicle[4]	22	Among individuals	Vézina and Williams, 2002
Zebra finch *Taeniopygia guttata*	Non breeding	First egg laid	22	Within individuals	Vézina and Williams, 2005
Zebra finch *Taeniopygia guttata*	Non breeding	First egg laid	24 (34)	Within individuals	Salvante et al., 2010

[1] Females caught during the breeding season with gonads size 1/50 of mean gonad mass. [2] Females caught in the spring before gonads recrudescence.
[3] Five time mean gonadal mass. [4] Day preceding first ovulation. [5] % increase in RMR above non-reproductive RMR values. Based on data corrected for mass by regression or ANCOVA. Values in brackets are based on estimates with no mass correction.

no measured females had begun laying (no eggs observed in the oviduct, M.A. Chappell pers. comm.), some had large yolky follicles (i.e., gonadal tissue mass five times the mean gonadal tissue mass of all measured females). Comparing predicted RMR estimates (based on a multiple regression predicting log RMR from log body mass and dry gonadal mass) for females with actively yolking ovarian follicles with those of females exhibiting fully regressed reproductive organs showed a 16% higher RMR in birds with large reproductive organs. This estimate is lower than measurements reported above for birds that were actively laying, but it is consistent with Nilsson and Raberg's (2001) observation of a 12% higher RMR in female great tits during ovarian recrudescence. Therefore, RMR appears to be increasing gradually during rapid yolk development and reproductive organ growth to culminate when the bird has an egg in its fully-grown oviduct (but see Vézina and Williams, 2002).

A third approach, based on daily energy expenditure (DEE) measurements has also been used to investigate energy investment in egg production. Ward and MacLoed (1992) used respirometry to measure DEE in Japanese quails (*Coturnix coturnix*), the only precocial species measured to date. Birds were maintained for 3 days in metabolic chambers with ad lib access to food and water. A 49% increase in DEE was observed in birds laying eggs each day compared to individuals that had not yet begun laying, and DEE was positively related to daily energy deposited in the eggs. In a later study, Ward (1996) measured DEE with doubly labeled water in barn swallows *Hirundo rustica* that were either producing eggs, incubating or provisioning nestlings. In this case, egg production had no significant effect on DEE variation when compared to the other breeding stages and was not related to egg energy content or clutch size. In a similar study, also using doubly labeled water, Stevenson and Bryant (2000) reported contrasting results in free-living, egg-producing great tits. Controlling for the effect of ambient temperature, a significant positive relationship between DEE and egg mass was found in one year but the relationship was reversed the following year, which they reported as offering poor breeding conditions.

DEE integrates energy expended in all aspects of a bird's activity budget, including behavioral adjustments to compensate for energy demanding activities such as egg production (see below, Williams and Vézina, 2001; Vézina et al., 2006; Williams et al., 2009; Salvante et al., 2010). Therefore, discrepancies in estimates of egg production costs are perhaps to be expected between studies that are using only DEE to estimate costs of egg formation. Furthermore, measures of DEE are not directly comparable to estimations based on RMR variation. Clearly, measurements on more species throughout the altricial-precocial spectrum, using a standardized approach such as measurement of resting metabolic rate during the non-breeding and egg production stages, are required before generalized interpretations of the energy costs of producing eggs can be made. Measurements of the energetic costs associated with egg production should also be undertaken in a variety of species exhibiting a wide range of body masses and egg sizes (relative to body mass) in order to examine how these parameters may affect reproductive energy investment in birds. For example, non-passerine species that lay relatively large and yolk-rich eggs (e.g. galliforms, waterfowl and seabirds) that develop over a longer time period (5–30 days, Roudybush et al., 1979; Astheimer et al., 1985; Astheimer and Grau, 1985; Astheimer and Grau, 1990, Alisauskas and Ankney, 1994; Esler, 1994; Gorman et al., 2007; Schneider, 2009) relative to small passerines species (e.g. 2.5–4 days; Ricklefs, 1974; Badyaev et al., 2005) may potentially experience different energy demands for egg formation. Laying a large clutch does not increase daily energy demand but extends total duration of the energy investment (Nager, 2006). Therefore seasonal changes in egg size within or between clutches in some species (Christians, 2002) could also reflect specific energy investment strategies adjusted to seasonal changes in local breeding conditions.

Knowing that egg production in birds has a measurable energetic cost begs the question, what drives the increase in metabolic rate measured during egg formation? To date, there has been no clear answer to this question but a few studies have improved our understanding of the phenomenon. At the inter-individual level, variation in the mass of the oviduct, the organ responsible for egg albumen and shell formation, has been shown to correlate positively with RMR in egg laying house sparrows ($r^2 = 0.30$, Chappell et al., 1999), European starlings ($r^2 = 0.18$, Vézina and Williams, 2003) and zebra finches ($r^2 = 0.23$, Vézina and Williams, 2005a). Although variation in oviduct mass explains at best 30% of RMR variation during egg production, it is important to note that oviduct mass is also correlated with egg size, at least in European starlings (Ricklefs, 1976; Vézina and Williams, 2003). Furthermore, Christians and Williams (2001a) found that oviduct mass ex-

plains approximately 21% of the egg's albumen protein content in that same species. Taken together, these observations suggest that generating a large oviduct, despite the associated metabolic cost, may be advantageous for female birds as it may allow for laying larger, better quality eggs (Vézina and Williams, 2003), which likely improves early chick survival (Williams, 1994; Christians, 2002; Wagner and Williams, 2007). However, in addition to the added weight, maintaining a large oviduct between breeding attempts may be maladaptive due to its associated energy demands. This could explain why this organ begins to regress rapidly from the ovary to the cloaca after the last ovulation while the last follicle is still progressing down the oviduct, even though the bird may breed again in the same season (Vézina and Williams, 2003; Williams and Ames, 2004).

Whether individual females can fine tune the size of their oviduct to influence egg size and quality is unknown. However, several species show an intraseasonal decline in egg size with laying date (Christians, 2002) and recent evidence suggests that females of some species can voluntarily adjust egg size to mate quality (Cunningham and Russel, 2000; Uller et al., 2005). Therefore, given the reported range of flexibility in oviduct mass (Table 1) and given the fact that its recrudescence is under hormonal control (Yu et al., 1971), it is reasonable to hypothesize that females may be able to modulate part of their physiological reproductive investment through adaptive phenotypic flexibility in oviduct size and function. More research is needed to test this "oviduct flexibility" hypothesis.

Other aspects of egg production physiology have also been studied with regard to their possible contribution to the metabolic cost of egg formation, but no other obvious energy demanding processes have been identified. During egg formation, estrogens synthesized in the newly-grown ovary stimulate the liver to produce the two major yolk precursor macromolecules, vitellogenin (VTG) and yolk-targeted very-low-density lipoprotein (VLDLy) (Bergink et al., 1974; Deeley et al., 1975; Wallace, 1985; Walzem, 1996; Williams, 1998). Once produced, VTG and VLDLy are secreted into circulation and are then taken up by the ovary by receptor-mediated endocytosis and processed within the ovarian follicles into yolk, the nutrient and energy source for the developing avian embryo (Bernardi and Cook, 1960; Wallace, 1985; Stifani et al., 1988, reviewed in Williams, et al., 2001). Nager (2006) reviewed body composition data for females actively laying eggs and observed an emerging pattern for a larger liver in 6 out of 9 studies

based on 7 species. Liver mass has also been shown to correlate positively with plasma vitellogenin in one of two years in European starlings (Christians and Williams, 1999). However, liver mass was found to vary independently of laying RMR in three consecutive years in the same species (Vézina and Williams, 2003), and liver maximal oxidative capacity was reduced in female starlings producing eggs (Vézina and Williams, 2005b). Furthermore, active yolk precursor production triggered by exogenous estrogen administration did not result in increased RMR in zebra finches (Vézina et al., 2003). Therefore, yolk precursors appear to be energetically inexpensive to produce, and this may explain why females forming eggs apparently produce yolk precursors in excess and saturate ovarian follicle receptors during rapid yolk development (Williams 2000, 2001; Williams et al., 2001).

Egg production involves other processes that may contribute to the metabolic cost of egg formation which have not been investigated. One on them is yolk uptake rate by the ovarian follicles. Yolk uptake rate correlates with final yolk size (Christians and Williams, 2001b), and VTG/VLDLy-receptor mRNA expression level in the ovarian follicle entering the rapid yolk development stage (i.e., F3) is positively correlated to the masses of the first laid egg and the largest developing ovarian follicle (i.e., F1) within the same clutch (Han et al., 2009). To date, the energetic cost of follicular yolk uptake rate, including biosynthesis of yolk precursor receptors, and the question of whether females can modulate egg size by reversibly varying yolk uptake rate remains to be studied. Females also have the capacity to modulate egg quality and alter offspring viability by varying yolk content as a function of constraints encountered during egg formation (e.g. hormones: Schwabl, 1993; Groothuis et al., 2005; Love et al., 2005, 2009, Carere and Balthazart, 2007; Love and Williams, 2008; antibodies: Hasselquist and Nilsson, 2009; antioxidants: Biard et al., 2009). The amount of energy invested in relation to egg composition and quality may therefore be related to an individual's immediate and future breeding effort (e.g. provisioning low quality chicks) and remains to be studied.

3.2   Males

The energetic cost of gonadal development and function in males has received much less research attention than in females. Bioenergetic models based on tissue energy content suggest that the cost of testicular recrudescence is low and represents less than 2% of BMR (King, 1973; Walsberg, 1983). However, this approach

for estimating metabolic energy requirement of reproductive organs has been contested as it only considers tissue energy content and ignores synthesis, maintenance and function costs (Nilsson and Raberg, 2001; Vézina and Williams, 2002). Furthermore, actual empirical measurements using respirometry on females differ considerably from predictions generated by bioenergetic models based solely on the energy content of their reproductive tissues (Vézina and Williams, 2002). We are aware of only one study that has empirically investigated the effect of gonad size on metabolism in male birds. Chappell et al. (1999) found a significant correlation between RMR and gonad mass in reproductive male house sparrows. Difference in testis size translated into a 29% higher mass-independent RMR in males with the largest gonads (maximal gonad mass 1.5 times average mass) relative to that of males with the smallest organs (considered non-reproductive). The reported effect of gonad mass on metabolism in male house sparrows is therefore comparable to maximal energy investment measured in egg producing females (27% increase in RMR in great tits; Nilsson and Raberg, 2001).

Chappell et al's (1999) finding clearly contrasts with recent data reported by Caro and Visser (2009) where testicular recrudescence triggered by artificial changes in photoperiod was not related to RMR of captive great tits maintained under two thermal regimes. Because cold treatment (8°C) induced a 20% increase in RMR but no effect on testicular growth, the authors concluded that gonad recrudescence was a process requiring relatively little energy (but see also Silverin et al. 2008 for effect of temperature on testis growth). A low energetic cost of testicular recrudescence and function is certainly compatible with observations of males growing testes weeks before females begin developing their reproductive organs (Caro et al., 2005, 2006, 2009) and maintaining mature testes for the whole breeding season (Table 2). However, in this specific case, the testes had not reached maturity by the time RMR was measured (Caro and Visser, 2009). Therefore, a possible relationship between testicular size and RMR in fully reproductive male great tits cannot be excluded and remains to be studied. Although the effect of circulating testosterone levels on BMR remains controversial (Wikelski et al., 1999; Buttemer and Astheimer, 2000; Buchanan et al., 2001; Buttemer et al., 2008) other aspects of male reproductive activity (e.g. behavioral changes including courtship singing and mate guarding) may also generate physiological changes associated with an increased

RMR during this period.

4   The Impact of Reproductive Effort on Energy Budgets: Reproductive Flexibility

Whether avian testicular growth and function is energetically costly or sufficiently constraining to elicit reversible physiological or behavioral adjustments to balance energy budgets remains unclear and requires further research. However, recent studies using captive zebra finches as a model system suggest that energy investment in egg production can lead to such observable changes in females. The next sections therefore focus on case studies highlighting phenotypic flexibility in relation to reproductive investment by female zebra finches.

4.1   Behavioral flexibility: The first line of defense

With reported increases in RMR of 22%–27%, egg production in birds may be considered a low-cost activity when compared to total energy expended on a daily basis. Ward (1996) found no differences in average DEE of barn swallows either producing eggs, incubating or provisioning nestlings. However, as will be discussed below, comparing population average DEE in this context is misleading because it masks variation related to individual reproductive investment and compensation strategies (see Vézina et al., 2006; Williams et al., 2009).

Five independent studies on captive zebra finches maintained at room temperature with *ad lib* access to food have shown a reduction in locomotor activity ranging from 40% to 65% during the period of egg production (Houston et al., 1995; Williams and Ternan, 1999; Vézina et al., 2006, Williams et al., 2009; Salvante et al., 2010), and the recorded decrease in activity has been shown to coincide with the onset of rapid yolk development in females (Williams and Ternan, 1999; Vézina et al., 2006). This phenomenon is not limited to zebra finches, however, as reduced activity has also been reported in free-living willow flycatchers *Empiodonax traillii* during egg formation (Ettinger and King, 1980), and female ruddy ducks *Oxyura jamaicensis* have been found to increase resting time during the same period (Tome, 1991).

The effect of this behavioral adjustment on a female's DEE (measured by doubly labeled water) has been investigated twice over two successive breeding attempts within the same females (Vézina et al., 2006; Williams et al., 2009). In both studies, reduced locomotor activity

was interpreted as a behavioral strategy to compensate for the energy costs associated with egg production. As found by Ward (1996) in barn swallows, average DEE of female zebra finches did not change between non-breeding and egg-laying stages (Vézina et al., 2006; Williams et al., 2009). However, there was marked inter-individual variation in the initial egg production investment (measured as RMR variation in females during egg laying), and the changes in locomotor activity were negatively correlated with egg producing females' RMR (Vézina et al., 2006). In other words, the level of energy compensation was adjusted to the individual investment, as females investing the most in egg production were also showing the largest reduction in activity. This latter finding paralleled a previous report of a negative relationship between clutch size and locomotor activity in laying zebra finches (Williams and Ternan, 1999). Behavioral flexibility therefore allowed birds to compensate for egg production costs and, perhaps not surprisingly, no changes or even decreases in average energy intake (measured as food consumption) have been detected in association with egg formation in this species under favorable conditions (Houston et al., 1995; Williams and Ternan, 1999, Vézina et al., 2006; Salvante et al., 2010). Consequently, balancing the energy budget through behavioral flexibility was suggested as a means to avoid large variation in DEE in females actively producing eggs (Vézina et al., 2006).

Vézina et al. (2006) and Williams et al. (2009) also showed that behavioral energy reallocation was individually variable and led to a range of effects on DEE, from negative changes from the non-breeding to the egg-laying stage (i.e. overcompensation) in some individuals, to additive effects (i.e. net increase in DEE) despite behavioral energy savings, in others. Both individual investment, measured by intra-individual variation in RMR, and compensation strategy (i.e. effect on DEE) were shown to be repeatable between breeding attempts (Vézina and Williams, 2005a; Williams et al., 2009), a finding which suggests that individual females tend to maintain their reproductive effort from one breeding attempt to the next. However, the link between consistency in energy investment and reproductive output is not as clear. Although, as in many species (reviewed by Christians, 2002), clutch size and egg size were repeatable among individual females (Williams et al., 2009), a positive relationship between egg-laying DEE and clutch size was found during the first breeding attempt (Vézina and Williams, 2005a) but was not confirmed in the following attempt (Williams et al., 2009).

Behavioral flexibility seems to be relatively common in birds facing energy constraints. For example, in addition to reproductive costs, reduced activity has been observed in birds facing thermoregulatory challenges (e.g. Cherel et al., 1988; Salvante et al., 2010), experiencing food limitation (e.g. Meijer et al., 1996; Dall and Witter, 1998) and undergoing feather molt (e.g. Austin and Fredrickson, 1987; Robin et al., 1989). This may be the simplest and fastest way to decrease energy expenditure and may represent the first line of defense when facing energy constraints before engaging in, perhaps slower and more costly, reversible changes in physiological function.

However, balancing energy budgets through reductions in locomotor activity might not always be a feasible option in natural conditions. This may be especially true in female birds wherein gonadal recrudescence and egg formation take place before the seasonal peak of food abundance (Perrins, 1996) and likely require increased foraging activity. In such cases, what other mechanisms are available for females to balance their energy budget? Several recent studies investigated energy compensation strategies in captive birds by experimentally increasing work for food rewards, thus preventing energy savings through reduced activity. A common finding was phenotypic flexibility at the physiological level as birds typically reduced nighttime resting metabolic rate (Bautista et al., 1998; Deerenberg et al., 1998; Nudds and Bryant, 2001; Wiersma and Verhulst, 2005; Wiersma et al., 2005).

4.2 Physiological flexibility: When behavioral adjustments are not enough

Although one can easily measure behavioral flexibility in response to the energetic costs of reproductive investment, perhaps more challenging is to study how birds can use phenotypic flexibility at the physiological level to adjust components of reproductive investment itself. Two recent studies (Salvante et al., 2007, 2010) suggest that female zebra finches facing conflicting constraints during egg production make physiological compromises in an attempt to maintain reproductive output.

Salvante et al. (2007) combined the energetic cost of producing eggs with increased thermoregulatory requirements. Using a repeated measures design, zebra finches were acclimated and bred at both 7°C and 21°C. Birds increased food intake by 45% in the cold as a result of higher daily energy demands but no changes in body condition, egg mass or mass of egg components (i.e., yolk, albumen and shell) were recorded. Ambient

temperature had little effect on egg quality with no significant changes in egg lipid content and 5% more protein in the yolks of eggs laid in the cold. Reproductive success was not reported as some of the eggs were collected for composition analysis. However, unpublished data suggest no temperature effect on hatching and fledging success of the remaining eggs (K.G. Salvante unpublished data). A shift in the composition of females' circulating plasma lipid was found where cold acclimated birds produced less yolk-targeted VLDL while maintaining total blood VLDL constant. Presumably, females increased the proportion of generic VLDL to support energy requirements of non-reproductive functions. Interestingly, while females laying in the cold maintained egg size, they produced eggs at a slower rate and invested less in terms of total production. Indeed, these birds took longer to produce their first egg (0.5 more days), laid smaller clutches (by 0.4 eggs), laid at a slower rate (reduced laying rate by 0.05 eggs per day) and skipped laying on more days (0.7 days vs. 0.5 days) than when maintained in the warm environment. Salvante et al. (2007) suggested that females laying in the cold had been digestively constrained, despite the increase in food intake, and were thus limited in the energy available to cope with both thermoregulatory and egg production costs. Therefore, they defended egg size at the expense of laying rate.

Egg size in birds is often a highly repeatable trait that varies more among females than within individual females (Christians, 2002). In fact, within-individual variation in egg size has a significant effect on chick survival and may incur long-term fitness costs in terms of offspring future fecundity (see Wagner and Williams, 2007). Although birds producing eggs in limiting environments can be nutritionally or energetically constrained, they nevertheless appear to maintain a certain minimal egg size. For example, Nager (2006) reported that only 41% of studies supplementing food to breeding birds resulted in larger eggs (calculated from Table 1 in Nager 2006). Christians (2002) reported a similar value of 36%, but also found that food restriction alone had no effect on egg size in the species investigated. While constraints experienced by females during egg production may affect egg quality without changing egg size (Heaney et al., 1998, Nager et al., 2000; Williams and Miller, 2003), adjustments in provisioning may later compensate for this effect (e.g. Nager et al., 1999). Consequently, individual females would benefit from "defending" a certain minimal egg size to maintain embryo viability when faced with constraining energy de-

mands during egg production. When resources are plentiful or of better quality (e.g. protein content, Nager, 2006) however, they should increase their investment and reproductive output. One way of doing this is producing larger eggs.

The Salvante et al. (2007) study involved birds maintained under ad lib food conditions and suggests that females "defended" egg size at the expense of egg production rate when faced with combined egg-production and thermoregulatory challenges. Other studies investigating temperature effects on reproductive output of free-living passerine birds do offer some support for this hypothesis (but see Christians, 2002). For example, the rate of laying has been positively related to ambient temperature in great tits (Lessells et al., 2002) and blue tits (*Parus caeruleus*, Yom-Tov and Wright, 1993), and Ojanen et al. (1983a) found the energy content of eggs to be positively related to temperature in pied flycatchers *Ficedula hypoleuca*. Other species seem to modulate egg size in response to thermoregulatory challenges. Indeed, egg size was reported to correlate positively with temperature in European starlings (Ojanen et al., 1981), pied flycatchers (Ojanen, 1983a), collared flycatchers (*Ficedula albicolis*, Hargitai et al., 2005), great tits (Ojanen et al., 1981; Nager and van Noordwijk, 1992; Pendlebury and Bryant, 2005) and blackbirds (*Turdus merula*, Magrath, 1992). Collectively, these observations suggest that birds use behavioral and physiological flexibility to strategically adjust their reproductive investment as a function of the interaction between the available resources and ecological constraints.

In their second study, Salvante et al. (2010), went a step further and measured, together with locomotor activity budgets, the metabolic cost of cold acclimation, the cost of producing eggs when acclimated to cold and warm conditions, as well as the metabolic rate of non-breeding and egg-laying individuals actively producing heat (under cold conditions). According to previous observations (see Table 3), egg production alone involved a 24% increase in RMR, was associated with a 64% reduction in locomotion and induced no change in food intake. Cold acclimation alone resulted in a 96% increase in RMR, a 72% decrease in locomotor activity and a 71% increase in food intake. However, when producing eggs, birds living in the cold showed no further decrease in locomotor activity and no change in RMR in association with egg formation. There was in fact an 11% *decrease* in RMR between non-breeding and egg laying stages when metabolic rate was measured under

cold challenge. Cold-acclimated birds also exhibited a 22% *decrease* in food intake when going from non-breeding to actively producing eggs. Body temperature measurements confirmed that cold acclimated egg laying birds did not use hypothermia as a means of saving energy. Therefore, with no further behavioral energy savings possible (no further decrease in locomotion), internal energy reallocation at the physiological level (Ricklefs and Wikelski, 2002; Moore and Hopkins, 2009) must have taken place for the birds to form eggs while decreasing total daily energy expenditure (based on reduced food intake) and RMR (Salvante et al., 2010). Salvante et al. (2010) suggested that downregulation of both reproductive and non-reproductive physiological systems must have happened for their birds to reduce daily energy intake (i.e. overcompensation) while producing eggs in the cold.

Down-regulation of non-reproductive physiological systems could have taken the form of a reduction in the size of non-reproductive organs (McKechnie, 2008). However, Nager (2006) reviewed studies where body composition data collected during the non-breeding and egg laying stages were compared within species and found little support for this hypothesis. In fact, the digestive organs (gizzard, pancreas and intestines), heart, kidney and lungs appeared to vary inconsistently between reproductive stages in many species. Two of these studies (Christians and Williams, 1999, Vézina and Williams, 2003) also considered among-year variability in non-reproductive organ size, and both studies reported inconsistent findings among years. However, it should be noted that none of these studies involved birds forming eggs in the cold. Alternatively, down-regulation of non-reproductive systems could take the form of reduced tissue metabolic intensity. However, although this has been shown in some species (Piersma et al., 2004; Selman and Evans, 2005; Vézina and Williams, 2005b; Rønning et al., 2008), more research is needed to test whether variation in metabolic intensity is used as a way to reallocate energy between physiological systems (e.g. Selman and Evans, 2005; Vézina and Williams, 2005b; Ronning et al., 2008) and to quantify the energy savings from such physiological down-regulation.

In reproductive systems, down-regulating the rate of organ recrudescence and egg formation could have allowed for the maintenance of egg size at the expense of a longer time to begin laying and a slower egg laying sequence in cold-acclimated zebra finches. Like other species in natural conditions, captive non-breeding female zebra finches maintain atrophied reproductive organs that must be developed to produce eggs (Williams and Martyniuk, 2000). A longer time period before laying the first egg could therefore result from a slower rate of reproductive organ recrudescence in females. Given the known metabolic cost of oviduct growth and maintenance (Chappell et al., 1999; Vézina and Williams, 2003), developing this organ at a slower pace may be a source of energy savings. Female zebra finches laying eggs in the cold did not change egg size but reduced the rate at which their eggs were produced (Salvante et al., 2007). If yolk uptake rate is an energetically costly process, then decreasing the number of yolk precursor receptors on the ovarian follicles would down-regulate the rate of ovarian follicle development (e.g. Salvante et al., 2007). This would require less yolk-targeted VLDL in circulation to saturate follicle receptors and, as suggested by Salvante et al. (2007), would allow females to increase the proportion of circulating generic VLDL to support the energetic requirements for thermogenesis. This would be a way to save energy without compromising egg size and viability. Further research is needed to test this hypothesis.

5 Phenotypic Flexibility in Reproductive Effort and Fitness

All evidence of early reproductive phenotypic flexibility discussed above is based on one model system: zebra finches breeding in controlled conditions with *ad libitum* access to food. It is obvious that more data are needed from other model systems, including studies focusing on male reproductive physiology and energetics. Physiological adjustments have been demonstrated several times at later stages of reproduction in other model species. For instance, incubating king penguins *Aptenodytes patagonicus* switch off digestion in the days before hatching (Gauthier-Clerc et al., 2000; Thouzeau et al., 2004). This prevents food from being degraded and allows the adult to feed its chick by regurgitation while the other parent is at sea. Black-legged kittiwakes *Rissa tridactyla* decrease self-maintenance costs (i.e. BMR) during incubation and chick-provisioning by reducing the size and energy consumption of internal organs such as the kidney (Bech et al., 2002; Rønning et al., 2008). However, very little information is available on how flexibility is used by birds in the early stages of reproduction. Probably one of the biggest challenges ahead is to find out how phenotypic flexibility associated with early reproductive investment translates to natural conditions and how it may relate to fitness.

We believe that future studies should ask how be-

havioral and physiological flexibility may be used to balance energy budgets and improve fitness when birds in the early phases of breeding are faced with natural and perhaps conflicting constraints such as thermoregulation and other demanding activities. We hypothesize that birds should always use behavioral adjustments first as a rapid and low cost way to balance energy budgets. However, behavioral flexibility may be limited under natural conditions and compensation between physiological systems may often be required.

Experiments with zebra finches suggest that females are consistent in their minimal reproductive output and effort as shown by significant intra-individual repeatability in egg size and clutch size (Williams,1996), egg laying RMR (Vézina and Williams, 2005a), egg laying DEE and energy compensation strategies (Vézina et al., 2006; Williams et al., 2009). Furthermore, females in Salvante et al's (2007, 2010) studies showed high repeatability of most indices of reproductive effort across multiple breeding attempts in the cold (egg size 79.4%, clutch size 37.5%, time to first egg 40.6%). Future research should ask whether consistent individual reproductive effort is a generalized phenomenon among bird species. Egg size is a repeatable trait (Christians, 2002) and could reflect females defending minimal investment through varying levels of ecological constraints between breeding attempts. However, the fact that repeatability in reproductive parameters is not 100% (average values for egg size 69%, clutch size 39% from Table 1 in Christians 2002) means that individuals do, to some extent, change their investment between breeding attempts. This variation is also a form of individual flexibility, and future studies could ask whether the most flexible individuals achieve better lifetime reproductive success. Flexible adjustments could also be dependent on life-history decisions, where phenotypic changes and energy investment during a breeding attempt would be influenced by whether or not individuals would breed again in the same season or by the intensity of breeding effort in the following years. These sorts of questions could be addressed with long-term databases where known individuals have been followed throughout their lives.

More experimental studies are also needed where up-regulation of non-reproductive functions (e.g. increasing workload for food, Wiersma and Verhulst, 2005; Wiersma et al., 2005; immune challenge, Martin et al., 2002; Love et al., 2008, temperature challenge, Salvante et al., 2007, 2010) during the early phases of breeding are implemented. Combining various types of conflict-

ing demands should help reveal different levels of physiological flexibility and tradeoffs as well as different outcomes in terms of reproductive output.

If females engaged in reproduction do "defend" their minimal investment, then one would expect down-regulation in non-reproductive functions when available energy is too limited to support all systems by simply reallocating energy by behavioral changes. When this is associated with long-term fitness consequences (e.g. Nager et al., 2001; Visser and Lessells, 2001), then physiological flexibility incurs a reproductive cost. Therefore, the challenge is to find out which systems may be compromised to support investment in reproduction and to determine the consequences of this flexibility in terms of reproductive success and survival. Life-history theory (Stearns, 1992; Roff, 2002) has generated a considerable number of studies interested in the potential trade-offs between manipulated breeding effort and other physiological functions such as immunity, condition, oxidative defense and self-maintenance (e.g. Oppliger et al., 1996; Ots and Horak, 1996; Deerenberg et al., 1997; Siikamaki et al., 1997; Horak et al., 1998; Cichon et al., 2001; Wiersma et al., 2004). However, few have investigated flexibility in non-reproductive parameters during the initial reproductive investment phases of gonadal recrudescence and egg formation, a time when resources may be monopolized to support the extreme changes occurring in the reproductive system (but see Williams et al., 2004; Wagner et al., 2008 a, b).

The "choice" of what system is used to balance energy requirements likely depends on a variety of factors affecting the relative long-term costs of down-regulating specific functions. For example, several studies have suggested that birds trade off immune function to support breeding efforts (e.g. Gustafsson et al., 1994; Norris et al., 1994; Oppliger et al., 1996; Ots and Horak, 1996; Sheldon and Verhulst, 1996; Deerenberg et al., 1997; Siikamaki et al., 1997; Horak et al., 1998; Bourgeon et al., 2006; Knowles et al., 2009), but the prevalence of pathogens in certain areas may make this strategy maladaptive and could prevent certain species or populations from doing so (Ardia, 2005). In such cases one would suspect another, perhaps more appropriate, short-term dispensable function to be down-regulated (e.g. oxidative defense; Wiersma et al., 2004). Depending on the requirements, there could also be a combination of systems that are down-regulated. Physiological tradeoffs are likely very dynamic and, as others have done before us (Seebacher, 2005; Barcelo et al., 2009; Moore and Hopkins, 2009), we call for studies using an

integrated approach, combining observations at multiples levels of organization.

6   Expanding Research Horizons

Studies on fitness consequences of reproductive effort generally ignore events taking place between reproductive attempts. Typically, experimenters manipulate reproductive investment by adding or removing eggs or chicks and measure variables such as return rate of adults the following year (Nager, 2006). Yet, evidence suggests that ecological demands occurring during reproduction and other life-history stages (wintering and migration) are physiologically linked and may interact to affect fitness (review by Webster et al. 2002, Webster and Marra 2005 and Norris and Marra 2007). Winter conditions in both tropical and northern latitudes may be relatively harsh with measurable effects on survival of species wintering in these areas (Brittingham and Temple, 1988; Marra and Holberton, 1998; Strong and Sherry, 2000; Gill et al., 2001; Marra and Holmes, 2001; Olson and Grubb, 2007). The main wintering constraint appears to be food availability (Jansson et al., 1981; Brittingham and Temple, 1988; Grubb and Cimprich, 1990; Sherry et al., 2005, Brown and Sherry, 2006), which can be aggravated by a cold and variable environment in northern resident species (Brittingham and Temple, 1988; Lahti et al., 1998; Doherty and Grubb, 2002). Poor wintering conditions and habitat quality have been shown to negatively affect physiological condition, stress level and survival (Brittingham and Temple, 1988; Rogers et al., 1993; Lahti et al., 1998; Marra and Holberton,1998; Strong and Sherry, 2000; Marra and Holmes, 2001; Doherty and Grubb, 2002; Brown and Sherry, 2006), and this may translate into later migratory departure and arrival on the breeding grounds and lower reproductive success (e.g. Marra et al., 1998; Norris et al., 2003; Saino et al., 2004; Gunnarsson et al., 2005). The common denominator of these carry-over effects is likely a compromised physiological condition (Norris and Marra, 2007).

Clearly, both wintering ecological conditions and individual breeding effort in the spring have the potential to affect physiological condition and performance during subsequent life-history stages. These carry-over effects should be considered in studies investigating phenotypic flexibility in relation to breeding investment and performance. However, studies on migratory birds are limited by their ability to follow individuals throughout their breeding and wintering ranges (Webster et al., 2002; Webster and Marra, 2005; Norris and Marra, 2007). Perhaps the best approach to begin to understand this complicated system is therefore to study non-migratory species that are traceable year-round or to design "seasonal" experiments with captive models.

7   Concluding Remarks

In birds the annual recrudescence of reproductive organs and the process of egg formation can be energetically costly, especially when these processes occur in sub-optimal environmental conditions and coincide with other energetically-challenging activities, including thermoregulation. We hypothesize that, as a first line of defense, birds use behavioral flexibility to rapidly decrease energy expenditure and meet these energetic demands. However, if behavioral flexibility is not feasible or the energy saved is not sufficient to balance their energy budgets, birds may then use physiological flexibility to deal with these energetic constraints. The use of behavioral and physiological phenotypic flexibility during reproduction likely has an effect on fitness as birds trade off activities that contribute to either reproductive success or survival, including reproductive investment, immunity, physiological condition and self-maintenance. To study these fitness consequences, reproductive phenotypic flexibility must be examined in the context of a bird's entire life history because environmental conditions, carry-over effects from other stages and previous reproductive attempts all influence the relationship between current reproductive phenotypic flexibility and lifetime fitness.

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