Mechanisms of Life History Evolution

The Genetics and Physiology of Life History Traits and Trade-Offs

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CHAPTER 10

Mechanisms of nutrient-dependent reproduction in dipteran insects

Alan O. Bergland

10.1 Introduction

Reproductive output, along with development time and lifespan, are the core parameters of an organism's life history. Together, these three parameters allow us to predict an individual's fitness and, by extrapolation, the growth rate of a population. Ultimately, natural selection should act to maximize fitness (Fisher 1930) and as a consequence these life history traits will respond in a correlated fashion (Robertson 1968).

The study of life history traits has repeatedly demonstrated that they show reduced genetic variation relative to putatively neutral characters such as morphological traits (Roff 2002). Presumably, reduced genetic variation in fitness components is due to the constant action of natural selection to maximize fitness. Although genetic variation in life history traits is generally low, it is still present in many populations. The presence of genetic variation for life history traits is possibly due to mutation–selection balance (discussed in Charlesworth and Hughes 2000), life history trade-offs (see several chapters in Part 6 of this volume), or some form of balancing selection such as genetic overdominance or, more likely, environmentally dependent marginal overdominance (e.g., Chapter 18). In this last scenario, environmental variation affects life history traits but not all genotypes are affected the same way. For instance, one genotype may do very well in one environment but very poorly in another; an alternative genotype may have the opposite pattern. Such a scenario can lead to the stable persistence of these two, hypothetical, genotypes. If these environments affect genotypic performance by altering life history traits then genetic variation will likely be observed.

The persistence of genetic variation in life history traits due to marginal overdominance is plausible given the sensitivity of many life history traits to the environment (Roff 2002, Hodin 2009). In general, the three major environmental variables affecting life history traits are photoperiod, temperature, and nutrition. Photoperiod, at least for many organisms living in seasonal environments (e.g., Chapter 9), plays a major role in determining the timing of development and reproduction (cf., Chapter 18). For these species, alterations in the timing of life history transitions affect the length of the growing season and consequently the number of reproductive cycles per year. In many organisms, notably ectothermic animals, exposure to variable temperatures affects development time, reproductive output, and lifespan. This effect is mediated by changes in the rate of metabolic and catabolic processes that are direct functions of temperature. Finally, nutrition affects life history traits by altering the rate and duration of larval growth and by directly limiting resources available for reproduction and somatic maintenance (Chapter 11). The biology of nutrient-dependent reproduction is reasonably well understood and is mediated by a complex set of interactions between molecular processes, morphology, and intraspecific interactions.

The goal of this chapter is to integrate what is known about the molecular, morphological, and behavioral basis of one aspect of an organism's life history: reproduction. In particular, I will focus on recent developments that have been made in understanding the mechanistic basis of nutrient-dependent reproduction in dipteran insects. Although I will be focusing on dipteran insects, it is reasonable to hypothesize that many of these mechanisms are shared among more divergent animals.

This chapter will be divided into three main sections. The first section will examine the relationship between larval nutrition and adult reproduction via growth and will focus on two related processes. First, I will discuss how nutrition affects the physical size of the adult and how body size and other allometric correlates directly relate to reproductive capacity. Second, I will discuss how larval nutrition provisions the adult with nutritive resources necessary for reproduction.

In the second section of this chapter, I will focus on the relationship between adult nutrition and reproduction. In this section, I will cover the role of the sensory, digestive, and endocrine systems and their role in reproduction. Finally, I will conclude the chapter by highlighting recent findings that integrate advances in the mechanistic basis of nutrient-dependent reproduction with the predictions that evolutionary theory makes about the dynamics of life history evolution.

10.2 Larval nutrition and reproduction

For Dipterans, larval nutrition affects female reproduction by mediating various aspects of adult body size. Environmentally induced variation in body size and other allometric correlates affect fecundity through at least four mechanisms. First, larval nutrition affects ovary size, which is a direct determinant of reproductive capacity. This effect appears to be universal amongst Dipterans. Second, larvally acquired nutrients are often necessary for adult reproduction and thus the extent of larval nutrition directly affects the number of eggs that can be provisioned. Third, adult body size is directly related to adult meal size in many Dipterans. Meal size affects the ability of adults to provision eggs, and thus affects fecundity. Finally, because larval nutrition affects body size it consequently affects male–female interactions, which are size-dependent for many Diptera. Size-dependent mating can negatively affect fecundity because larger males can cause greater physical harm to females during copulation and potentially invest fewer resources into each female. Below, I discuss these four mechanisms in detail.

10.2.1 Ovary size

The insect ovary is composed of repeated structures called ovarioles (reviewed in Hodin 2009) and each ovariole is capable of simultaneously producing an egg. Therefore, given sufficient adult nutrition, ovariole number sets an upper limit on reproductive rate and capacity (David 1970).

The positive relationship between ovariole number and fecundity is present within and amongst species of Diptera (reviewed in Honek 1993). For instance, variation in ovariole number within populations of *D. melanogaster* is positively correlated with fecundity (David 1970, Bergland and Tatar, unpublished data). Likewise, variation in ovariole number amongst populations of *D. melanogaster* is correlated with fecundity (e.g., Boulétreau-Merle *et al.* 1982). Finally, variation in ovariole number amongst closely related Drosopholids (reviewed in Hodin 2009) is positively correlated with fecundity.

While there is abundant genetic variation in ovariole number, it is also highly sensitive to the larval environment (e.g., reviewed in Hodin 2009) and in particular to larval nutrition (e.g., Bergland *et al.* 2008 and references therein). Hodin and Riddiford (2000) showed that for *Drosophila melanogaster* larval nutrition affects ovariole number by modifying the rate of differentiation of a specialized set of cells at the anterior tip of the ovariole—the terminal filament cells. Interestingly, this variable rate of differentiation occurs during the wandering stage, a period when larvae are no longer feeding. This observation suggests that the ovariole number is set by endocrine or paracrine signals from another tissue that is growing in direct response to larval nutrition. It is plausible that this tissue may be either the larval fat body or the prothoracic gland, two organs that have recently been identified as regulators of body size in insects (reviewed in Mirth and Riddiford 2005).

This hypothesis is substantiated by the results of Bergland *et al.* (2008), who performed a quantitative trait locus (QTL) mapping study of nutritional plasticity of ovariole number in *D. melanogaster*. They identified at least nine QTL affecting ovariole number and ovariole number plasticity in response to larval nutrition. One pair of epistatically interacting QTL contains the imaginal disc growth factors, *Idgf1*, *Idgf2*, *Idgf3*, and *Ras85D*. The IDGFs are secreted by the larval fat body and affect imaginal disc growth (Kawamura *et al.* 1999). *Ras85D* is a member of the RAS signaling pathway, which, in conjunction with *PI3K* activity in the prothoracic gland, affects nutrient-dependent insulin signaling in the larval fat body (Mirth and Riddiford 2005). Thus, it is plausible that nutrient-dependent insulin signaling alters IDGF secretion, which in turn affects the rate of terminal filament differentiation during the wandering stage. Further work is needed to test this hypothesis.

Orgogozo *et al.* (2006) have also suggested that genetic variation in insulin signaling underlies differences in ovariole number between two closely related species, *D. simulans* and *D. sechellia*. The latter species is endemic to the Seychelles Islands and has evolved resistance to the toxic *Morinda citrifolia* fruit, which it uses as its exclusive nutritive resource (discussed in Orgogozo *et al.* 2006). For unknown reasons, *D. sechellia* has evolved a nearly two-fold reduction in ovariole number (Orgogozo *et al.* 2006) and concomitant reduction in fecundity (R'Kha *et al.* 1997). Line crosses between these two species initially identified autosomal factors underlying differences in ovariole number (discussed in Orgogozo *et al.* 2006). Fine-scale QTL mapping has localized these loci to a region on chromosome 2 and to two epistatically interacting regions on chromosome 3. Orgogozo *et al.* (2006) point out that the insulin receptor (*InR*) lies within one of these epistatic QTL on chromosome 3 and hypothesize that genetic variation at this locus has contributed to differences in ovariole number. This hypothesis is consistent with the observation that mutants in the insulin signaling pathway have decreased ovariole number (e.g., Tu and Tatar 2003).

10.2.2 Meal size

Larval nutrition affects adult body size, which subsequently determines how much food adults can ingest. Adult meal size, of course, will determine the amount of resources available for reproduction. The relationship between body size, meal size, and fecundity is best understood in blood feeding mosquitoes such as *Anopheles* spp. where blood meal size is directly mediated by abdomen size (e.g., Roitberg and Gordon 2005).

In mosquitoes, the relationship between meal size and body size is determined by sensory mechanisms in the abdomen (Gwadz 1969). Mosquitoes, being relatively opportunistic feeders, will gorge themselves on blood when they find a suitable host. Individuals gauge how much they have eaten by the expansion of their abdomen, the extent of which is sensed by a set of nerves that innervate the abdomen. When these nerves are severed, adults will feed until their abdomen explodes (Gwadz 1969). This rather dramatic behavior demonstrates that the control of meal size in mosquitoes is purely physical. However, physiological mechanisms will determine how many meals are necessary before sufficient resources are attained for reproduction in anautogenous species.

10.2.3 The effects of mate size

Nutrient-induced plasticity in body size affects males as well as females (Chapter 4). For some dipteran species, male body size affects access to females through competition (e.g., McLachlan and Allen 1987) and may also directly affect female fecundity. The best-known examples of the latter are in *D. melanogaster*, where a negative correlation between male body size and female reproductive output exists, particularly for reproductive output during early and mid life (Pitnick 1991, Pitnick and García-González 2002). In these studies, male body size was experimentally altered by manipulating larval density, thus larval nutrition may have indirect effects on female fecundity through male body size.

Pitnick (1991) suggested a behavioral mechanism for this phenomenon. For many insect species, males compete with each other for access to mates and typically larger males win. Because large males might have access to multiple females in a short period of time, and for many male insects sperm is limited (discussed in Bretman *et al.* 2009, Wigby *et al.* 2009), it could be beneficial for large males to distribute relatively smaller ejaculate to each female, thereby increasing the male's total reproductive fitness but potentially decreasing an individual female's reproductive potential. Small males, in contrast, might only have access to females on rare occasions. Therefore, it is plausible that small males take advantage of their infrequent mating and release most of their stored ejaculate at a single time. Small males copulate (Pitnick 1991, Kelic *et al.* 2007) for a longer period of time than large males and thus it is possible that a longer copulation duration results in a larger ejaculate, thereby increasing reproductive success per female. This hypothesis is plausible given recent evidence (Bretman *et al.* 2009, Wigby *et al.* 2009) that copulation duration is positively correlated with the quantity of at least one oviposition stimulating protein, sex peptide, which is transferred from males to females upon mating (see Section 10.3.1 for a longer discussion of the mode of action of sex peptide, SP).

The relationship between male size and female reproductive output in *D. melanogaster* may be mediated by phenotypic plasticity in female size (Lefranc and Bundgaard 2000, but see Pitnick and González 2002). Lefranc and Bundgaard (2000) found that male body size was negatively correlated with female fecundity only in large and medium-sized females. However, the size-dependent interactions between males and females with respect to fecundity has not been confirmed by independent replication (Pitnick and González 2002). Given that size-dependent assortative mating occurs in some Diptera (e.g., Sisodia and Singh 2004 and references therein), further research on the relationship between male and female size with respect to fecundity is warranted.

10.2.4 Larval nutrition and teneral reserves

It would be safe to say that larvally acquired resources are used for reproduction in all Diptera, yet the extent to which they are necessary for reproduction varies amongst different lineages. The quantity and quality of adult nutrition certainly determines how important larvally acquired resources are. For instance, many species of mosquitoes do not feed on blood during adulthood or prior to the first ovarian cycle. For these mosquitoes, larval nutrition totally determines the extent of reproduction.

This is the case for some populations of the pitcher-plant mosquito, *Wyeomyia smithii*, which are completely autogenous (non-blood-feeding). These populations are found at northern latitudes, where larval resources are not limited due to low intraspecific competition (Lounibos *et al.* 1982) and abundant larval resources (Bergland *et al.* 2005). For larvae that experience these relatively benign conditions, adults emerge with enough resources to reproduce and hematophagy is not observed. However, in southern populations larval densities can be much higher and adults that experience intense intraspecific competition as larvae are unable to provision eggs without a blood meal. Thus, for this species autogeny is both genetically fixed (north versus south) and plastic (nutrient-dependent in southern populations).

Autogenous–anautogenous polymorphisms are present in many other species of mosquito (Attardo *et al.* 2005). In some species, this polymorphism is environmentally induced, but in others it is under strict genetic control. For example, in the Asian tiger mosquito, *Aedes albopictus*, researchers were able to artificially select for autogeny from a stock laboratory population (Mori *et al.* 2008). From that selection experiment, Mori *et al.* (2008) were able to produce a completely autogenous strain, generate a mapping population by intercrossing with an anautogenous strain, and map three to four QTL affecting this autogenous behavior. These loci each contribute less than 10% of the total genetic variation within this mapping population, suggesting that other loci of small effect or epistatically interacting loci also contribute to autogeny. Although the position and effect of loci controlling autogeny/anautogeny polymorphisms have not been determined for other mosquito species, most evidence suggests that in each species many loci segregate alleles that can confer autogeny in primarily anautogenous species (Attardo *et al.* 2005).

Dipterans that must feed as adults in order to reproduce nonetheless utilize larvally acquired resources for adult reproduction. In blood-feeding mosquitoes, larvally acquired resources are an important component of reproductive output. This is especially true during the first gonotropic cycle, which is prior to blood feeding in some anautogenous species. Zhou *et al.* (2004 and references therein) found that for *A. aegypti*, larvally derived carbohydrates, lipids and amino acids make up roughly 70–99% of egg protein and lipids found in the first clutch of eggs. The remainder came from sugars acquired during early adult feeding. While subsequent gonotropic cycles will utilize blood-meal-derived resources, it has not been determined how long teneral reserves will persist in adults. Furthermore, it has not been determined whether components of larvally acquired resources are non-renewable in anautogenous mosquitoes.

There do not appear to be any non-renewable, larvally acquired resources in *D. melanogaster*. Furthermore, larvally acquired resources make a very small contribution to total reproductive output. A set of studies by Min *et al.* (2006) and O'Brien *et al.* (2008) found that larvally acquired carbon and nitrogen are used for early life reproduction (i.e., prior to day 10) and these larvally acquired resources only make up less than 15% of the total carbon and nitrogen in the eggs during this short timespan. After day 10, there were virtually no larvally derived resources found in eggs. Thus, in contrast to other insects such as Lepidoptera (e.g., O'Brien *et al.* 2002) and Dipterans mentioned above, teneral reserves in this species do not play an important role in provisioning eggs nor do there seem to be any irreplaceable, larvally acquired resources.

10.3 Adult-acquired resources

For anautogenous species of Diptera, variation in adult resources directly affects the extent of egg production (reviewed in Hodin 2009). Variation in the acquisition of adult resources is determined by present nutritional status (i.e., hunger), her ability to find food, and the conversion of those resources into the proteins used to provision eggs. Hunger is mediated by neuroendocrine signals, which stimulate the drive to locate resources. The ability to locate food as an adult is controlled by sets of olfactory and gustatory receptors located in the sensory neurons spread throughout the adult body. Once food has been identified, enzymes throughout the gut digest these complex proteins and sugars, which are then transported to the haemolymph. Changes in sugar, fat, and protein in the haemolymph ultimately affect egg production by altering hormonal balances that alter the production of yolk proteins. In this section, I will discuss recent work identifying the specific molecular bases for each of these behavioral and physiological processes and their relation to fecundity.

10.3.1 Hunger

Presumably, the feeling of hunger is required in order to initiate the search for food. In adult Diptera, hunger is mediated by two factors. First, and quite obviously, hunger is mediated by nutritional status. To date, the specific physiological mechanisms mediating the relationship between hunger and nutritional status have been elucidated in larval *D. melanogaster*. It is likely, however, that the same mechanisms mediate the relationship between nutritional status and hunger in adults. In larvae, response to hunger (as measured by feeding rate after bouts of starvation) is suppressed by the release of *Drosophila* insulin-like peptides (*dIlps*) from the brain (Wu *et al.* 2005). Wu *et al.* (2005) further demonstrate that high levels of *dIlps* maintain food selectivity, whereas low levels of *dIlps* (i.e., conditions of starvation) promote feeding on suboptimal media. The effect of *dIlps* on food preference is caused by interactions with set neurons in the brain, which are sensitive to neuropeptide F (NPF, Wu *et al.* 2005). Thus, through *dIlps* and NPF signaling, food acquisition rates and food preference are altered in response to hunger.

Second, sexual status (i.e., mated versus virgin) alters food acquisition rates. During copulation, males transfer SP in the seminal fluid and this peptide stimulates adult feeding (Carvalho *et al.* 2006), along with other post-mating behaviors such as oviposition and mating refractoriness. Presently, it is unclear how sex peptide induces these coordinated behaviors. Specifically, it is unknown if sex peptide affects all of these processes directly or if sex peptide initiates one of these behaviors (e.g., feeding), which in turn stimulates another (e.g., oviposition). To date, data suggest both of these general processes cause the coordinated action of reproduction and feeding in response to sex peptide.

Sex peptide is thought to cause post-mating behaviors through two general processes. First, neurons that terminate in the reproductive tract are responsive to sex peptide through the sex peptide receptor (*SPR*; discussed in Clyne and Miesenböck 2009). Genetic ablation of *SPR* in these neurons inhibits oviposition after mating compared to wild-type controls. The neuronal action of sex peptide on reproduction could be subsequently mediated by neuronal connections in the abdominal ganglion. Some of the *SPR* neurons terminate in the abdominal ganglion, which is known to affect ovulation (the release of mature eggs) through the production of octopamine (see below; Monastirioti 2003). However, flies lacking *SPR* in their reproductive tract neurons lay more eggs than wild-type females mated to males lacking sex peptide. These results suggest other modes of action for sex peptide with respect to reproduction.

Sex peptide could also stimulate post-mating behaviors through action on other tissues or neurons elsewhere in the adult. Sex peptide is present in the haemolymph following mating and is known to stimulate the production of juvenile hormone (JH) by the corpora allata *in vitro* (reviewed in Kubli 2003). JH is well known to positively regulate egg production (Flatt *et al.* 2005, see below and Chapter 13). Thus, differences in reproduction between females lacking *SPR* in the reproductive tract and those mated to males without sex peptide could be due to the absence of JH induction by sex peptide.

Current evidence suggests that increased feeding following exposure to sex peptide (Carvalho *et al.* 2006) is most likely a functional consequence of reproductive activity (or, at least, of oogenesis). These data come from experiments that have examined the role of sex peptide on feeding in genetically sterile *ovo*^{D1} flies. *ovo*^{D1} is a dominant allele that causes sterility by inhibiting germline stem cell (GSC) maintenance; after the first division of the GSC, no new oocytes are produced and thus, in *ovo*^{D1} flies, the ovary does not act as a nutrient sink. Barnes *et al.* (2008) demonstrated that *ovo*^{D1} flies exposed to sex peptide do not feed after mating. This result suggests that production of vitellogenic oocytes are required for post-mating induced feeding. This interpretation implies that reproduction (or ovulation) depletes nutritional reserves, inducing hunger and subsequently feeding.

However, adult feeding might also be directly affected by JH. Recently, a putative JH binding protein encoded by the gene *takeout* (*to*) has been associated with adult feeding rate and other phenotypes (Meunier *et al.* 2007 and references therein). Reductions in *to* levels increase feeding rate and locomotion in males and females (Meunier *et al.* 2007). Meunier *et al.* (2007) also demonstrated that, in males, exogenous application of the JH analog, methoprene, rescues wild-type locomotor behaviors. While this effect was not observed in females, it does not preclude an interaction between *to* and JH in regulating feeding in females. *to* is also expressed in the gustatory neurons located in the mouthparts of *D. melanogaster* and has been implicated in taste perception after bouts of starvation. In contrast to wild-type flies, *to* mutants do not display increased activity of sugar-sensitive neurons following starvation (Meunier *et al.* 2007). Thus, *to* might be an important integrator of mating-status-induced feeding (via JH via sex peptide), taste perception, and reproductive output.

10.3.2 Finding nutrition

Olfactory and gustatory receptors are necessary for reproduction because they allow females to identify resources used for egg production and to identify oviposition substrates. For many dipteran species, identification of adult resources and oviposition substrates is clearly differentiated in time and space. For instance, in anautogenous mosquitoes, females must find a suitable mammalian host, obtain a blood meal, digest it, and then find a location to oviposit. Thus, the chemical cues that signify food are distinct from those that identify oviposition substrate. For other dipteran species, such as those in Drosophilidae, this distinction is not as clear. Adults feed at the same locale as they oviposit and this raises the possibility that the chemical cues that allow adults to identify food sources are the same as those that identify oviposition substrate. However, recent work indicates that these cues are perceived by female *D. melanogaster* through distinct chemosensory mechanisms. How, then, do Dipterans find food and oviposition substrate?

Dipterans sense chemical cues through taste and smell receptors located in sensory neurons throughout the head, legs, and abdomen. Two large gene families, the gustatory receptors (GRs) and the odorant receptors (ORs), enable individuals to identify taste and smell. In dipteran species studied to date, ORs contain roughly 60–70 members and the GRs contain roughly 70–80 members (reviewed in Touhara and Vosshall 2009). Each receptor has a high affinity for a small set of ligands (Touhara and Vosshall 2009), and through combinations of receptors, individuals are able to perceive complex chemical environments. The ability to perceive such complex chemical cues enables species to display very subtle host and oviposition preferences.

For instance, in mosquitoes, CO_2 in combination with other perspired chemicals allows female mosquitoes to find hosts. Host specificity is determined by sensitivity to particular combinations of emanations released by a host. For instance, anthropophilic mosquitoes are attracted to lactic acid, which is a major component of human sweat (reviewed in Takken and Knols 1999). Attraction to lactic acid is potentiated by CO_2 (Dekker *et al.* 2005), which is sensed by two GRs, *GPRGR*22 and *GPRGR*24. To date, the OR or GR that senses lactic acid has not been identified.

Female mosquitoes use very different chemical cues to identify oviposition substrate. First, females utilize volatile chemicals released by bacterial decomposition of organic matter to identify suitable oviposition sites (Millar *et al.* 1992). However, the specific receptors sensing these chemicals have not been identified. Female mosquitoes are also attracted to chemical cues deposited by conspecific females upon oviposition, but the mechanisms regulating this type of aggregation have not been identified. Although the mechanisms for host-seeking and oviposition behavior have not been fully worked out, it is clear that the sensory mechanisms mediating these behaviors are biologically distinct.

For species of Diptera that utilize the same resources for adult nutrition and oviposition, such as members of the Drosophilidae, it is not clear *a priori* that females use distinct chemical cues in order to identify adult resources and oviposition sites. However, recent work suggests that different sensory mechanisms are used in these two processes. Work in *D. melanogaster* and related species demonstrates that females are attracted to by-products of yeast fermentation, such as acetic acid, ethyl acetate, and ethanol (e.g., Ruebenbauer *et al.* 2008). However, yeast odor *per se* does not influence oviposition (Libert *et al.* 2007). Rather, it appears that the choice to oviposit on a particular substrate is governed by chemosensory neurons located in the ovipositor (Yang *et al.* 2008). This choice is mediated, in part, by the expression of an insulin like peptide, *dIlp*7. The role of *dIlp*7 in mediating the choice to oviposit suggests that oviposition is a secondary process following nutrient identification, acquisition, and digestion.

10.3.3 Oogenesis and ovulation

Given that a female Diptera has sufficient nutrition, and has found a mate and oviposition substrate, how does she make and release eggs? The process of egg production, or oogenesis, is primarily controlled by the action of three classes of hormones,: JH, 20-hydroxyecdysone (20E), and the *insulin-like* peptides (*dIlps*). These hormones have well-known, coordinated effects on metamorphosis (reviewed by Mirth and Riddiford 2005) and there is a growing body of literature demonstrating that the proper balance of at least JH and 20E is necessary for oogenesis. The coordinated actions of JH and ecdysone are thought to also be mediated by at least two biogenic amines, dopamine and octopamine. Octopamine is also known to play a crucial role in ovulation. Below, I shall briefly discuss some recent work elucidating the relationship between these four hormones and oogenesis and ovulation; further discussion of the role of JH on insect life histories can be found in Chapters 4, 5, and 13.

Oogenesis is a complex physiological process that is composed of several distinct processes, including germline stem-cell division and differentiation, yolk production (vitellogenesis), and the construction of the eggshell itself (chorionogenesis). Of these three processes, nutrition is known to play a major role in germline stem-cell division, differentiation, and vitellogenesis. Adult-acquired nutrition alters the secretion of neuronally derived *dIlps*, which directly stimulate the asymmetric division of germline stem cells (i.e., division into one self-renewing germline stem cell and one cell, called a germline cyst, destined to become an egg) in a niche-independent fashion (reviewed in Drummond-Barbosa 2008). The germline cyst must undergo four rounds of cell division to become a 16-cell cyst, at which point it acquires yolk and develops into a mature egg. Acquisition of yolk by the 16-cell cyst is mediated by cyst autonomous insulin signaling, that is, cysts lacking functional *InR* fail to acquire yolk (reviewed in Drummond-Barbosa 2008).

While the uptake of yolk by germline cysts is mediated by autonomous insulin signaling, nutrient-dependent production of yolk itself appears to be regulated in a more complex fashion. Yolk proteins (either vitellogenin or yolk peptides, YP) are upregulated upon feeding (discussed in Attardo *et al.* 2005) and the upregulation of these genes is mediated by the joint actions of 20E and JH. For instance, nutritionally deprived *D. melanogaster*, which normally have low levels of YP synthesis, increase YP production upon exogenous application of 20E and methoprene, a JH analog (reviewed in Postlethwait and Shirk 1981). 20E increases YP transcription through the action of ecdysone receptor/ultra spiricle transcription factor complex, which directly binds to the ecdysone response element 5′ of the YPs (Bownes *et al.* 1996). The action of JH on YP production is more elusive, partly due to the general difficulty identifying the molecular modes of JH action (Jones and Jones 2007). However, it is generally thought that JH, synthesized in the corpra allata upon nutrient acquisition, directly stimulates early fat body and ovarian YP production, while concomitantly stimulating 20E production by the ovary. This ultimately leads to sustained YP production in the fat body (reviewed in Gruntenko and Rauschenbach 2008).

The levels of 20E and JH must be appropriately balanced, however, to successfully stimulate oogenesis (Soller *et al.* 1999). For instance, in *D. melanogaster* under starvation conditions, 20E titers rise (Terashima *et al.* 2005) and JH titers fall (Tu and Tatar 2003, cf. Rauschenbach *et al.* 2004). These changes in hormonal titers are correlated with apoptosis of early oocytes (Terashima *et al.* 2005) and with the repression of YP production. Exogenous application of 20E without simultaneous application of JH under normal nutritive conditions also reduces egg production (Soller *et al.* 1999, Terashima *et al.* 2005). Additionally, exogenous application of JH under starvation conditions elevates 20E titres and increases the number of mid-stage oocytes compared to non-JH-treated flies (Terashima *et al.* 2005).

The interaction between 20E and JH on vitellogenesis may be modulated by the action of two biogenic amines, dopamine and octopamine (reviewed in Gruntenko and Rauschenbach 2008), which are thought to regulate the metabolism of 20E and JH in an environment and age-dependent fashion. Evidence to date suggests that dopamine inhibits JH degradation in early life and under normal environmental conditions. As an individual ages or when she experiences unfavorable environments, Gruntenko and Rauschenbach (2008) propose that dopamine ceases its inhibitory role in JH degradation and starts stimulating JH degradation. The net effect of this switch in dopamine action would be to reduce egg production. Gruntenko and Rauschenbach (2008) further suggest that this switch is mediated by a transition from inhibitory to stimulatory dopamine receptors in the fat body. However, to date there is no evidence that these receptors are expressed in the fat body (Draper *et al.* 2007). Exogenous application of octopamine has also been noted to affect JH degradation (reviewed in Gruntenko and Rauschenbach 2008), but its modes of action are not known.

Octopamine has another very important role in reproduction in that it acts to stimulate ovulation, or the movement of the egg from the ovary through the oviduct. Initially, the role of octopamine on ovulation was observed by noting that *D. melanogaster* with octopamine deficiencies produce eggs but do not release them (Monastirioti 2003). When these flies are fed octopamine or when octopamine synthesis is rescued in neurons that innervate the ovary, ovulation proceeds normally (Monastirioti 2003). Ovulation, stimulated by octopamine, is thought to occur via contractions of the muscles surrounding each ovariole and by relaxation of the muscles surrounding the oviduct (Middleton *et al.* 2006).

Qazi *et al.* (2003) have also suggested that the process of ovulation *per se* induces oogenesis. This process would also feedback on the endocrine system because it would deplete nutritional reserves and would thus alter behavior, inducing foraging. These coordinated processes are also induced by accessory gland proteins (ACPs, and notably SP) transferred from males to females during mating (see above). Further work is certainly needed to examine the interrelations of these ACPs, ovulation, oogenesis, and behavior in the Diptera.

10.4 The evolutionary genetics of reproduction: Future prospects

Many ecological, behavioral, morphological, and physiological factors affect reproduction in Diptera. This chapter has highlighted several of these key components, but there are still large gaps in our general understanding of dipteran reproduction. One particularly promising area of study will be identifying how genetic variation in the processes underlying reproduction vary amongst species (reviewed in Markow and O'Grady 2005, 2008) and amongst populations within species. Such information will be particularly interesting because it can be tied to environmental differences between populations and species, and potentially to the selective pressures causing phenotypic differentiation.

Work in this area is underway. For example, naturally occurring polymorphisms in the *D. melanogaster*'s *InR* have been associated with female fecundity as well as other life history traits (Paaby *et al.* 2010). These polymorphisms vary in a clinal manner, suggesting that this gene, and the associated phenotypes, are under contemporary natural selection. A similar story has been documented for reproductive diapause in *D. melanogaster* (see Chapter 18). Reproductive diapause in *D. melanogaster* is characterized by a strong resorption of vitellogenic oocytes upon exposure to cold temperatures. The ability of an individual to enter into reproductive diapause is controlled by naturally occurring polymorphisms in the *couch potato* (*cpo*) gene. These polymorphisms show latitudinal clines consistent with the action of natural selection (Chapters 13 and 18).

Identification of naturally occurring genetic polymorphisms that affect reproduction and other life history traits is a crucial step in understanding their short- and long-term evolutionary dynamics. For instance, application of population genetic tests to the natural polymorphisms in *InR* (Paaby *et al.* 2010) suggests that this gene is evolving under directional selection. However, this is just one example and it would be wrong to assume that other naturally occurring polymorphisms affecting life history traits are evolving by similar mechanisms. Thus, in order to understand the evolutionary history of genes affecting fitness-related traits much broader genomic-level perspectives are needed.

Fortunately, such opportunities are becoming available. The advent of high-throughput sequencing technologies will allow for the rapid and cheap genotyping of many individuals. This will facilitate more efficient association mapping of complex traits and will hopefully lead to the identification of point mutations affecting life history traits. With such association maps in hand, we will be able to further interrogate the population genetic patterns of these loci that are putatively under natural selection. This type of investigation may finally provide insight into a longstanding problem in life history evolution, namely why genetic variation in life history traits exists even though we expect natural selection to efficiently remove it.

10.5 Summary

1. Reproduction in Dipterans is an environmentally labile trait, which is strongly influenced by many environmental factors, including nutrition.
2. Nutrition affects reproduction in Dipterans by altering larval growth, and this affects body size and other allometric correlates. In females, larval growth conditions limit reproduction by altering ovariole number, a direct determinant of fecundity. Also in females, body size determines meal size and thus the availability of resources to provision eggs. In males, body size affects competitive ability and thus access to females. Competitive dynamics between males may alter a male's reproductive investment in females and subsequently alter his mate's reproductive output.
3. Adult-acquired resources affect reproductive output by limiting resources available for reproduction. Hunger, the ability to locate resources, and conversion of those resources into yolk mediate the relationship between adult-acquired resources and reproduction. Insulin, ecdysone, juvenile hormone,

and biogenic amine signaling underlie these behavioral and physiological processes.

4. The genetic and physiological determinants of nutrient-dependent reproduction are likely subject to natural selection. Most likely, this will erode genetic variation in these pathways. However, many studies have shown that genetic variation, while limited, does exist for life history traits, including reproduction. The identification of natural alleles conferring genetic variation in reproduction will help characterize the molecular evolution of these pathways and will help in our understanding of the processes that create and maintain genetic variation.

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