

Forum

Differential allocation and compensation: who deserves the silver spoon?

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It is well known that being given “silver spoons” can be beneficial to offspring, in the sense that conditions experienced early in life can have long-lasting consequences (Lindström 1999; Qvarnström and Price 2001). Traits expressed by parents often form a large part of the offspring environment. Life-history theory predicts that parents should adjust their current reproductive investment according to both the expected pay-off from the current attempt and the expected future reproductive events (Stearns 1992). Thus, for selection to favor increased investment, the cost of decreased survival or future reproductive success for the parent should be compensated by higher survival or reproductive success of the current offspring. Because offspring of diploid species have a mother as well as a father, a parent of either sex might benefit by adjusting its investment based on the phenotypic or genetic traits of its mate.

Since Burley's (1986) first formulation, this idea has been called differential allocation (DA). Burley's early studies focused on a particular aspect of the interaction between costs and benefits experienced by the mother and the father: In her hypothesis that an individual could benefit by increasing effort when mated to an attractive member of the opposite sex because this might enhance the ability to maintain the pair-bond with this mate now or in future breeding attempts (Burley 1986, 1988). The discrepancy between early work that focused on pair-bond maintenance and current much broader definitions is probably a healthy sign of progress in a field. Even so, in this paper, we would like to point out that the field is still plagued by differences between researchers in what they consider DA and in which direction they predict allocation of resources to vary. Particularly, the “compensation hypothesis” has recently been proposed as a mechanism that appears to make opposite predictions to the DA hypothesis, but as we shall show, there is much clarification needed before we can reach a stage where the core ideas are crisply stated and the relationships between various hypotheses are properly evaluated. We will show that similar clarifying work needs to occur in the development of theory as well as in empirical studies.

Differential allocation: what is it?

Burley's (1986) pathbreaking idea was based on work on a biparentally caring species, the zebra finch *Taeniopygia guttata*. She showed that both males and females had higher reproductive success if they were allocated leg bands with colors that were attractive to the opposite sex. As this manipulation increases attractiveness but should have no direct causal impact on survival or reproductive success, Burley (1986) as-

sumed that the effects were due to higher investment by the opposite sex when mated to an attractive mate. In a separate experiment she measured this investment (Burley 1988) using various proxies and found, again, support for DA. The high-quality parent can, in a sense, “demand” higher investment from his or her partner and consequently lower its own investment. It is noteworthy that Burley explicitly stated that DA “applies where mate choice involves both sexes,” and therefore did not restrict DA to a prediction of female investment only. She did also explicitly note that her hypothesis assumes biparental care (Burley 1988).

It is illuminating to contrast Burley's predictions with the now decade-old review of DA by Sheldon (2000). DA had, by this time, achieved its modern, broad definition: its premises are that “first, that parents tradeoff their current and future reproduction; and second, that the attractiveness of the mate affects the optimal tradeoff between these two components of reproduction” (Sheldon 2000 p. 398). This definition does not require biparental care; benefits of attractiveness could be genetic or superior mates could simply provide environments that are particularly suitable for offspring development (e.g., a male might defend a high-quality territory but not provide any paternal care). Also, there is no specific requirement that the reason to change investment in offspring is to maintain the pair-bond with a high-quality mate. DA can occur whenever allocation into offspring brings about benefits to a parent that depend on the traits of its mate and this can happen even if this mate was never to be seen again.

Support for the broad version of DA has been found mostly in birds (e.g., Cunningham and Russell 2000) but other studied taxa include arthropods (e.g., Kotiaho et al. 2003) and fishes (e.g., Kolm 2001). In an inclusive sense, some form of cryptic female choice (Thornhill 1983; Birkhead and Pizzari 2002) could also be seen as a form of DA (see also Sheldon 2000): differential feeding of young sired by an attractive male is not conceptually very different from preferentially nurturing eggs fertilized by superior males (Thornhill 1983). One could argue, however, that rejection of sperm of unattractive males (e.g., Pizzari and Birkhead 2000) is too far from differential maternal investment to count as DA as the offspring of unattractive males, who might receive less care, do not exist in the first place. Semantic nit-picking aside, these considerations show that there is a smooth transition from cryptic female choice to DA; as similar processes might operate in both, researchers would benefit from being familiar with process in both fields.

A very striking consequence of the broadening of the definition of DA from biparental systems to more broad usage that the field has simultaneously become “sex asymmetric.” Even though Sheldon (2000) explicitly emphasized that either the male or the female can adjust its investment based on mate attractiveness, subsequent work has strongly concentrated on maternal investment. “DA” as a topic search phrase yielded a total of 55 papers published 2000 or later (search conducted on 15 June 2009) that additionally satisfied the criterion of testing for an association between parental resource investment in relation to mate attractiveness. Forty-nine out of these 55 papers focused exclusively on maternal investment and male attractiveness. Three of the 6 papers that measured the reverse (paternal investment in relation to

female attractiveness) were studies of the same species, the rock sparrow, *Petronia petronia*.

Reproductive compensation: a true alternative?

There is another clear trend in the set of papers that purport to test DA: they tend to document increased parental investment when one's mate is attractive. This was part of Burley's (1986, 1988) original idea. Sheldon's (2000) definition quoted above makes no such directional prediction yet he, in the same paper, reports that "differential allocation is expected to be unidirectional with respect to mate attractiveness (i.e. more allocation when breeding with more attractive individuals)". Intriguingly, this statement appears to be based on no theory but on verbal arguments where one should take maximal advantage of a good opportunity (Sheldon discusses interest rates offered by banks) and on the wealth of evidence that had accumulated by then for positive correlations between investment by one sex and attractiveness of the other (Sheldon 2000). But could one not imagine that when offspring are likely to fare less well due to a less than ideal mate, a parent could be selected to compensate and try to provide the silver spoon precisely when the offspring need it most?

This is indeed what has been later found in studies of barn swallows *Hirundo rustica* (Saino et al. 2002), collared flycatchers *Ficedula albicollis* (Michl et al. 2005), house finches *Carpodacus mexicanus* (Navara, Badyaev, et al. 2006; Navara, Hill, and Mendonca 2006), pronghorn *Antilocapra americana* (Byers and Waits 2006) and—perhaps surprisingly given the history of DA—zebra finches (Bolund et al. 2009). In all the avian cases, the trait has been an aspect of maternal allocation into eggs (androgens, various antioxidants such as carotenoids, and overall egg size). In the case of pronghorn, females compensated for matings with a less attractive mate by elevating rates of milk delivery to their young (Byers and Waits 2006). Given the directional prediction stated by Sheldon (2000), it is easy to see why all these authors have reported their results with some surprise and emphasize that their findings are contrary to predictions of DA. In some cases, the authors have additionally returned to a considerably more restrictive definition of DA than Sheldon (2000) intended: "the differential allocation hypothesis [...] posits that females increase their investment into reproduction when mated to attractive males" (Michl et al. 2005; for another case of similar use see Rutstein, Gilbert, and Tomkins 2005).

All the above-mentioned studies use terminology related to the idea of "compensation" but only one of them (Byers and Waits 2006) refers explicitly to a compensation hypothesis. This hypothesis appears to have been developed simultaneously, yet largely independently, of the above studies: its roots are in the theoretical and empirical work by Patricia Gowaty and coworkers (Gowaty 2003, 2008; Bluhm and Gowaty 2004; Gowaty et al. 2007). We mention these papers separately from the others because the compensation hypothesis as coined by these authors is subtly different from the general compensatory idea above. According to Gowaty, individuals are selected to compensate by increasing reproductive investment when mated to nonpreferred mates (Gowaty et al. 2007; Gowaty 2008) rather than attractive mates. This distinction may be important if the individual preference is not the same as the consensus attractiveness of a partner (Gowaty 2008). The main reason attractive males may not be preferred is that their attractiveness might be based on exploiting a sensory bias and the attractiveness thus does not necessarily predict high viability of offspring (Gowaty 2008). One should remember, however, that offspring viability is not the only benefit possible. If attractiveness is heritable, then the production of "sexy sons" ("Fisher's sons effect") will influence parental

fitness (Kokko et al. 2006; Taylor et al. 2007). Because attractiveness of offspring may also be affected by parental investment (Qvarnström and Price 2001), parents could conceivably increase their fitness by investing more in their offspring when the genetic prospects for producing highly attractive offspring are good. Thus, the exclusion of attractiveness as a basis for reproductive investment decisions may be somewhat premature (see also Sheldon 2000 for the convoluted interaction of genetic quality and parental investment).

Individual researchers are of course free to describe their hypotheses using whatever phrases they find most fitting and exclude certain processes from their hypotheses—data will then show which hypothesis will be most supported. However, in the field of DA and reproductive compensation, we appear to have reached a somewhat unfortunate situation where this freedom has created abundant terminological confusion. To sum up the current messy state of affairs: 1) the compensation hypothesis as used by some explicitly do not refer to attractiveness of the mate, whereas others refer to compensation precisely when dealing with responses to attractiveness; 2) compensatory patterns of any type are routinely considered an alternative and opposing pattern to predictions of DA. In reality, if one takes Sheldon (2000) as the currently accepted definition of DA, the definition itself makes no prediction at all about whether investment by one sex should covary positively or negatively with attractiveness of its mate. That this is virtually never acknowledged is unsurprising given that Sheldon (2000) does not point it out but instead makes an explicit positive prediction, without connecting it to the definition; 3) definitions of DA have in some cases returned to be much narrower but in a different sense than what was used by Burley (1986, 1988): for example definitions by now have sometimes become sex-specific such that they consider maternal allocation only.

Will modeling help to decide who deserves the silver spoon?

The power of theory in evolutionary ecology is to make assumptions explicit which often help to clarify biologically relevant issues. Very recently the first model was published showing that both positive DA (by which we mean a positive relationship between own investment and attractiveness of one's mate) and reproductive compensation (the opposite pattern) may arise from the same principles: All that is needed is to adjust certain parameter values such as how much parents can alter offspring survival through changing their investment (Harris and Uller 2009). The importance of such a contribution to the debate cannot be overestimated because it provides the first formally derived predictions that either case can be based on the same life-history principles. Results from the model suggest that reproductive compensation should be relatively rare in nature and that positive DA should be much more common. Reproductive compensation was only found when the effect of female investment on offspring fitness was relatively low (Harris and Uller 2009).

So is the matter now settled? We shall argue that despite being a great step forward, the work by Harris and Uller (2009) does not directly resolve all the confusion there is in the literature and hence, we welcome much more work on this contentious issue. This should not be taken as a too harsh criticism: founding work, no matter how pathbreaking in the long term, rarely solves all the issues at hand in an instant. We would therefore like to point out 3 shortcomings that the field as a whole should consider: first, modeling so far has not commented on the terminological confusion that still persists; second, theory so far only considers a small subset of potential causal factors; and third, the pattern still remains that researchers appear not to be aware of all the work done in

the area. The combination of the second and third factor means that we should treat current predictions (e.g., that compensation should be rare) with caution.

Our first claim is easy to justify. Modeling has so far not resolved any of the persistent terminological confusion. There are only 2 models available so far: in addition to Harris and Uller (2009), we have found only one additional model, which addresses a rather specific hypothesis in which females increase the number of offspring under adverse conditions in the hope that at least some are able to cope with pathogen diversity (Gowaty 2008). These 2 models repeat the discrepancies mentioned above: both claim that DA is the phenomenon found when mate attractiveness covaries positively with own allocation and reject the idea of DA when a negative pattern is encountered.

Harris and Uller (2009) thus treat DA and compensatory patterns (which they term “reproductive compensation,” or RC) as mutually exclusive outcomes of a single process. We believe that the single-process viewpoint is valuable but simultaneously that an explicit recommendation of terminology is timely. We suggest it is better to use the broad definition of Sheldon (2000) for DA but ignore Sheldon’s hunch that DA also automatically implies positive covariation. Instead, the sign of covariation (more or less investment in offspring of attractive mates) should be treated as a question deserving empirical as well as theoretical investigation. Consequently, we recommend using the term “positive DA” when individuals invest more in offspring of attractive mates and “negative DA” when they invest less.

Because compensatory mechanisms are at work in the latter case, one might argue that reproductive compensation and negative DA are synonymous. We indeed recommend not restricting compensatory terminology to cases that avoid dealing with consensus attractiveness of a mate, but we would also like to point out that the phrase “compensation” in general refers to mitigating a loss. Compensation is linked to a type of adaptive reasoning (individuals compensate in order to improve on an unfortunate situation) not to any particular covariation pattern (when A is high, B is low). Consequently, it is unwise to restrict its use to negative covariation of any predefined set of traits. This point is made clear by the fact that adaptive reasoning based on compensatory responses might be usefully employed in cases that exhibit positive DA. The most obvious example of such a case occurs when an attractive male (with high potential for extrapair success) increases his mating effort at the expense of paternal care and his female has to make the best of a bad job by compensating for the lack of care. The net outcome is positive DA—more care by females paired to attractive males—but the adaptive reasoning would be hard to express without using the word “compensation.”

Our second claim is that theoretical work has not yet considered all aspects of DA. This, too, is easy to justify. The model of Harris and Uller (2009) considers that females adjust their parental effort in response to effects that males have on offspring survival. They thus only consider a sex-asymmetric situation. Although one could also reverse the labels “female” and “male” to claim otherwise, the 2 sexes in this model still do not both respond to each other. In other words, one sex evolves to respond to the other but simultaneous responses to each other are not included. Such game-theoretic considerations could have easily been seen to arise from the original formulation of biparental care (Burley 1986) but despite being published during a time with much advances of game-theoretic treatments in animal behavior research, this has never been followed up. Kokko (1998) modeled male behavior to show that attractive males may evolve to provide either more or less care than unattractive males (depending on the profitability of mating effort to gain extrapair offspring), but this work was neither phrased in a DA context nor considered

its game-theoretic nature as any adjustment by the female was not modeled.

There are also other limitations. In Harris and Uller (2009), females cannot remain mated to the same male in different breeding attempts, instead males are encountered randomly by each female and the original reason to invest in attractive males—maintaining the pair-bond (Burley 1986)—is not modeled. Finally, Harris and Uller (2009) assume that offspring survival is the only trait that responds to parental investment, and investment by the mother and the father have an additive effect on this trait: female fitness gains during any given reproductive bout equals the number of offspring “times” survival, where survival equals a baseline + difference caused by female behavior + difference caused by mate identity. This quantification of fitness excludes numerous aspects of reproduction, such as a how parents deal with the complexities of the quality–quantity trade-off in offspring production (Beckerman et al. 2006; Galeotti et al. 2006; Gowaty 2008; Leips et al. 2009), that biparental care might bring about synergistic (nonadditive) benefits to offspring survival (Kokko and Johnstone 2002), that offspring survival might be a non-linear function of care received (ultimately this must be true as survival cannot exceed 100%), that investment in offspring may only show its positive effects later in the life of offspring (Lindström 1999; Monaghan 2008) for example as improved attractiveness of offspring once they have reached maturity (Griffith et al. 1999), that such benefits typically depend on the sex of offspring (Lindholm et al. 2006), and that the investment level required to achieve a certain level of offspring fitness may depend on competition within each sex, for example, the mating skew (Bolund et al. 2009).

Our list of omissions in Harris and Uller (2009) may appear excessive up to being nihilistic. We do not mean to be overly negative: rather, we would like to contrast the state of affairs within DA research with that of sex ratio theory. That field has long ago advanced from verbal arguments, for example the Trivers–Willard hypothesis that high-quality parents should overproduce sons (Trivers and Willard 1973), to detailed examination of the underlying logic (e.g., Leimar 1996), with sufficient body of theory built-up by now that books summing up current research have large sections devoted to reviewing the theoretical developments to date (Hardy 2002). It is curious indeed that the entire field of DA has only one model to work with—and in this context one should also mention that allocation decisions can even link the 2 fields because biasing the sex ratio of offspring could occur simultaneously with a change in overall investment (Rutstein, Gorman, et al. 2005, see also Badyaev et al. 2005).

Our third claim is that theoretical work to date does not rectify the problem so far present in empirical papers, which researchers appear not to cite all relevant work. Harris and Uller (2009) consider compensatory solutions to be rare, and they cite Sheldon’s (2000) work to support the prevalence of this pattern in nature. However, this does not fit perfectly with the empirical evidence collected lately as more evidence of reproductive compensation has mounted in recent years. Yet, most of these appear not to have influenced the modeling as only a subset was cited in Harris and Uller (2009). Additionally, as Bolund et al. (2009) points out, many studies have designs of very low power, and therefore small chance of finding the compensatory phenomenon.

Will new work change the conclusions?

It is difficult to evaluate whether adding more real-world phenomena to models of DA would change the balance of positive and negative DA patterns. Whereas we have intentionally

highlighted recent cases of negative DA because of their conceptual importance, positive DA has remained a common finding (for recent examples see Head et al. 2006; Loyau et al. 2007; Bonato et al. 2009). More explicit treatment of why, and under what conditions, one or the other pattern might predominate certainly appears worthwhile.

So few aspects have been included in modeling work so far that the generality of conclusions can only be considered unknown. There are plenty of verbal arguments to work with. For example, as pointed out by Bolund et al. (2009), the amount of reproductive skew could be a crucial determinant of whether individuals should adjust effort upwards or downwards when mated to attractive individuals (Bolund et al. 2009). If only high-quality offspring have a reasonable chance of mating, as in a system with high reproductive skew, then one can only hope to produce such offspring when all good things coincide: one's mate should be attractive and then the offspring may still require a "boost" of receiving high parental investment in them. This increases the likelihood of finding positive DA. If on the other hand all offspring have a good chance of mating relatively independently of quality, negative DA may be more likely. It is then mostly in the interest of any parent to make sure that the offspring do not fall below the minimal threshold under which survival and mating becomes unlikely: only under poor conditions this is a real danger, thus warranting compensatory increases in parental care. Whether such intuition turns out foolproof in formal modeling remains to be investigated: for example, in biparental systems sexual conflict over care can considerably complicate the predictions. Under strong skew, for example, is maximal effort by both parents required before a very attractive offspring can be produced or does the effort by one parent allow the other one to invest less?

Empirical problems: which currency?

Lack of theory on which to base experiments is not the only lament an empiricist should voice in this field. Because the DA hypothesis is very general, it is not trivial to choose which characters to look at. DA has been tested with ornaments (e.g., Saino et al. 2001; Loyau et al. 2007), plumage coloration (Navara, Hill, and Mendonca 2006), body size (e.g., Kolm 2001; Kotiaho et al. 2003), song quality (e.g., Gil et al. 2004; Leitner et al. 2006), symmetry of a "sexy" trait (Forkman and Corr 1996; Swaddle 1996), age (e.g., Michl et al. 2005), size of a nuptial gift (e.g., Thornhill 1983), nest building behavior (Szentirmai et al. 2005), courtship behavior (Edvardsson and Arnqvist 2005), and a combination of several traits (Galeotti et al. 2006). Experimental studies that change the preferred characters (e.g., de Lope and Møller 1993; Johnsen et al. 2005) or add artificial ornaments that exploit existing sensory biases (e.g., Burley 1986; Gilbert et al. 2006) should always be interpreted keeping in mind that a lack of results may simply indicate that a wrong trait was selected as a correlate.

Some studies have consequently used different measures of preference as proxy for attractiveness in the opposite sex. Examples include previous reproductive success (Bolund et al. 2009), number of mates (Gwinner and Schwabl 2005), preference tests with several females (e.g., Cunningham and Russell 2000), and free mate choice compared with restricted mate allocation (Simmons 1987; Bluhm and Gowaty 2004). An alternative experimental strategy has been to food supplement some males in expectation that they will get in better condition and relate female parental investment to food regime of their partner (e.g., Wedell 1996; Helfenstein et al. 2008). Obviously, such manipulations should not be used without tests showing that they actually affect the attractiveness of the manipulated parent. Although this was not fully

accomplished in the above-cited studies, results still appear justified in the latter because females were shown to be more faithful to supplemented males (Helfenstein et al. 2008).

Likewise, the level of investment can also be in diverse currencies, and the empiricist again is faced with a choice of what to measure. Parental effort after hatching or birth, allocated in relation to partner attractiveness, played a central role in the original formulation of Burley (1986, 1988) and several subsequent studies (e.g., Limbourg et al. 2004; Johnsen et al. 2005; Matessi et al. 2009). By manipulating male attractiveness and cross-fostered young, Helfenstein et al. (2008) have also given an example where chick growth and fledging success function as a good indicator of parental posthatching investment because the differences found in such a design cannot be the result of genetic or prenatal parental effects. The size or number of offspring may also be adjusted to partner attractiveness. This has been investigated in a number of studies looking at egg or fetus size (e.g., Cunningham and Russell 2000), egg number (e.g., Head et al. 2006), the seasonal number of broods (e.g., de Lope and Møller 1993), or total brood mass (e.g., Kolm 2001).

A recent study of female freshwater crayfish is illuminating as it shows just how complex the interpretation of allocation patterns can become. In *Austropotamobius italicus* eggs sired by small sized males with large claws are bigger, whereas smaller more numerous eggs are laid when paired to large, small-clawed males (Galeotti et al. 2006). Variation in total clutch weight cannot be explained by either of these traits. The large eggs may be considered an example of positive DA but producing them comes with a cost of producing few of them, which some might argue is a negative allocation decision. The interpretation should depend on how egg size influence offspring fitness and the exact trade-off between egg size, number, and future female reproductive success.

Yolk composition is an example that some investment currencies are only available for one sex to alter. Despite the sex-neutrality of the DA hypothesis, certain currencies can only be predicted to be allocated by females according to the attractiveness of the male. Deriving detailed predictions from DA theory for becomes increasingly hard when moving from the size and number of eggs to egg composition. Although it is reasonable to assume that antioxidants (Saino et al. 2002) and immunoglobulins (Saino et al. 2001) have a positive effect on offspring quality, investment in hormones is particularly difficult to interpret. The effects of androgens, for instance, can be sex-specific (Groothuis et al. 2005), and they have been shown to have adverse effects on offspring of low-genetic quality, whereas offspring of high-genetic quality may experience benefits (Gil et al. 1999). Because androgens may be immunosuppressive (Groothuis et al. 2005), there is reason to think that androgens should be coupled with antioxidants to offset the detrimental effects (Safran et al. 2008).

The study of different currencies is essential to understand how allocation can vary to achieve different goals. If it is in a mother's interest to compensate for the low quality of her offspring, it will in most cases not be efficient to increase her number of offspring, but rather invest more in each. However, this argument is turned to its head by Gowaty (2008) who argues that a female mated to a nonpreferred male may benefit by increasing her number of offspring to increase the variance in their genetic composition, improving the chances that some will survive. (As we have explained above, Gowaty additionally makes a distinction between preferred and attractive, yet the opposite nature of the above arguments is unaffected by this.) Investment in one currency may be complemented by reduction or increases in other currencies by the same parent or by the partner. Specific predictions should be provided by theoretical models but until such predictions

have been found, empirical studies should keep an open mind to provide the best possible background for theoretical development. An example is provided by a recent study of yellow-legged gulls, *Larus michaellis*. Parents of both sexes adjusted their feeding effort to the manipulated red spot on their partner's bills, and this in turn was found to affect the investment decisions of the manipulated parents (Morales et al. 2009).

Future directions

We have already given several suggestions on future directions for theoretical development of this field, but to sum up, it is clear that the theory in this field is inadequate. There are many possible aspects of DA not included in the single model that exists and even though that model is a very valuable contribution complementary work is in great demand.

In contrast to the scant theoretical efforts in the field, there are now a large number of empirical studies testing the DA hypotheses. Evidence from several taxa exists by now (Sheldon 2000; Gowaty et al. 2007), but the strong emphasis on avian studies remains true to date. The generality of the hypotheses suggest that tests should be performed in a number of different species and the current imbalance in favor of avian species should be balanced. We have throughout our paper emphasized that the field would benefit from a broader consideration of issues that apply regardless of the taxon studied. To end on this note, we would like to suggest that plants may serve as good independent study organisms for these hypotheses. The selective embryo abortion hypothesis states that genotypes of low quality should be aborted and all resources should be allocated to embryos of high quality, an idea that has received some support (Korbecka et al. 2002). This mechanism is directly comparable to females producing more eggs for higher quality sires, and if this is correct, then depending on the mechanism, it may also be possible for plants—at least female plants or the female function of cosexual plants—to perform DA.

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