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The mechanisms of morph determination in the amphipod *Jassa*: implications for the evolution of alternative male phenotypes

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The proximal basis for and the maintenance of alternative male reproductive strategies and tactics are generally not understood in most species, despite the occurrence of male polymorphism across many taxa. In the marine amphipod *Jassa marmorata*, males differ in morphology as well as behaviour. This dimorphism corresponds to two contrasting reproductive strategies: small sneaker males or 'minors', and large fighter males or 'majors'. This study uses quantitative genetic analyses in conjunction with experimental manipulations to assess the relative importance of genetic versus environmental factors in the determination and maintenance of these alternative mating strategies. Heritability analyses indicated the reproductive phenotypes do not reflect genetic differences between dimorphic males. By contrast, morph determination was significantly affected by diet quality. Majors essentially only developed on high-protein diets. Field studies also identified a strong correlation between seasonal shifts in the relative proportions of morphs and changes in food (i.e. phytoplankton) quantity and composition, corroborating that diet cues the switch between alternative reproductive tactics. Moreover, the comparison of major and minor growth trajectories identified a heterochronic shift in maturation times between morphs, indicating that ecological selective pressures, rather than just sexual selection, may be involved in the maintenance of this conditional strategy.

Keywords: alternative reproductive tactics; amphipod; conditional strategy; heterochrony; male dimorphism

1. INTRODUCTION

The evolution of male polymorphism (i.e. distinct male morphs), in contrast to the elaboration of male characters associated with sexual dimorphism between the sexes (see the review in Andersson 1994), has not received much attention despite its relatively widespread occurrence (Gross 1996). Male dimorphisms have been documented in a broad range of taxa, including arthropods, fish, lizards and birds, and may involve differences in morphology, behaviour, physiology as well as life history (Gadgil 1972; Gross 1996). Male dimorphism is typically expressed as two discrete male morphs (Gross 1996) that correspond to alternative reproductive strategies. Major males or 'fighters' are large with elaborated secondary sexual characters and behave aggressively, fighting for access to potential mates. Minor males or 'sneakers' are usually smaller, lack or have reduced secondary sexual characters, such as male ornaments and weapons, and sneak matings instead of engaging other males.

The determination and maintenance of these alternative reproductive strategies may have either a genetic (e.g. Shuster & Wade 1991; Ryan *et al.* 1992; Lank *et al.* 1995), or environmental basis (e.g. Emlen 1994; Radwan 1995). For the genetic determination of alternative strategies, the average fitnesses among male types must be equivalent. However, if the dimorphism reflects a conditional strategy, where morph determination is determined by some environmental factor, fitness need not be equal among male morphs. Based on relatively few empirical studies, conditional rather than genetic determination of male morphs appears to be more common.

Males in the marine amphipod *Jassa marmorata* are dimorphic (figure 1), exhibiting both morphological as well as behavioural traits that reflect fighting versus sneaking reproductive strategies (Clark 1997; Kurdziel 1999). The sneaking reproductive behaviour of minor males is coupled with a small body size and a lack of exaggerated secondary sexual traits. Geometric morphometric analyses have statistically demonstrated that minors are morphologically more similar to females than majors (Kurdziel 1999). By contrast, major males use their elaborated claws in male to male combat, as well as for posturing during mate guarding to thwart other major males. Both sexes mate multiple times during their lifetimes (Kurdziel 1999; Clark & Caudill 2001), but females typically mate only once after each molt (i.e. multiple matings in females are sequential and there is no sperm storage). As females are only receptive during a short period of 1–2 h following molting (Borowsky 1985; Kurdziel 1999), competition among males can be intense. Fighting males remain perched upon the tube that females inhabit and physically wrestle other major males away from the female, whereas minor males slip under the surveillance and sneak matings. This species lives on hard substrates such as docks and pilings, reaching densities as high as 5000 ani-

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Table 1. Effects of food (*a*) quantity and (*b*) quality on developmental rates.
(In the food-quantity experiment, sex was nested within family and food level by necessity, as newly emerged juveniles cannot easily be sexed. Separate analyses were run for the two dependent variables, maturation time and number of molts to maturity. The results from non-parametric statistical tests were qualitatively identical to those from the ANOVAs. SS, sums of squares.)

variable	SS	d.f.	*F*	*p*
(*a*) effects of food quantity				
number of molts				
family	54.486	9	3.137	0.002
food quantity	8.849	1	4.586	0.034
family × food (sex)	36.904	26	0.735	0.817
maturation time				
family	828.495	9	2.006	0.063
food quantity	2864.117	1	62.410	< 0.0001
family × food (sex)	1651.885	26	1.384	0.120
(*b*) effects of food quality				
maturation time				
maternal diet	384.621	1	11.615	0.001
offspring diet	520.307	1	15.713	< 0.0001
maternal × offspring (sex)	444.101	2	6.706	0.001

mals per 10 cm^2; however, population density, as well as relative proportions of the male morphs, vary seasonally (Clark 1997; Kurdziel 1999).

Rather than making the 'best of a bad lot' (e.g. Eberhard 1982), the relative efficiency with which minor males gain access to females (Clark 1997; Kurdziel 1999) indicates that their fitness may be comparable with that of fighting males. This raises the possibility that the alternative mating strategies in *Jassa*, as in the marine isopod, *Paracerceis*, may be genetically determined. However, the pronounced seasonal shifts in the relative abundance of the male morphs indicate that the dimorphism in *Jassa* may be conditional, triggered by some environmental variable that fluctuates seasonally. To distinguish between these hypotheses, we used a combination of quantitative genetic analyses and experimental manipulations. We used parent–offspring regressions to determine whether morphological differences associated with the alternative mating tactics had a heritable basis. To examine possible condition-dependent effects that may arise through the increased energetic costs of producing an exaggerated claw and larger body in fighter males, we quantified the effects of diet quantity and quality on male morph determination using experimental manipulations. The effect of food quality on male morph determination was studied by varying the diets of the offspring themselves, as well as the diets of their mothers, to identify any possible maternal effects. We discuss the implications of the results for the evolution of alternative male reproductive phenotypes, and specifically, why a traditional focus on the phenotype itself, rather than its proximate basis, may lead to misleading interpretations about causation.

2. MATERIAL AND METHODS

All individuals of *J. marmorata* (Corophioidea: Ischyroceridae) were collected from a population at Stony Brook Harbor, NY during April and May 1997 and July 1998. The amphipods were reared at 23 °C under a 12 L : 12 D regime in glass beakers with aerated, filtered seawater (27‰) and a small piece of plastic window screen as the substrate. The amphipods were maintained on a mixed diet of live phytoplankton: the green alga *Dunaliella tertiolecta* (Chlorophyceae), the golden alga *Isochrysis galbana* (Prymnesiophyceae), and two diatoms, *Thalassiosira pseudonana* and *T. weissflogii* (Bacillariophyceae), at a total cell concentration of 6×10^5 cells ml^{-1} determined on a Coulter Multisizer II (algal species were chosen based on their occurrence in the field and ease of culture). *Artemia fransiscana* nauplii were added to the algal diet after the majority of amphipods had molted three times. Preliminary trials showed that this food ration was in excess of what the amphipods could consume in 2 days.

(a) *Heritability estimates*

To obtain a large number of virgin females for heritability analyses, one generation of amphipods was reared in the laboratory. The original stock population came from 50 gravid field-caught females that were held individually in glass beakers. When the offspring emerged from the marsupium, the external brood pouch, they were isolated from each female and randomly assigned to new beakers and reared at a density of 10 juveniles per beaker. Mature females (identified by the presence of developed brood plates) were isolated and kept in individual beakers. Thus, all females used to estimate heritabilities were of the same age and experienced the same environment.

Fifty virgin females were individually mated to either a major or minor field-caught male (i.e. 25 majors and 25 minors). Once eggs were visible in the marsupium, males were removed and preserved in 70% ethanol. Newly emerged juveniles were transferred to clean beakers, reared until sexual maturity and then preserved individually in ethanol. Body size (distance from tip of rostrum to tip of telson) was measured on the parents and offspring, and thumb size was measured as the perpendicular distance from the tip of the thumb to the claw in males. All morphological measurements were made with a Wild stereomicroscope equipped with an ocular micrometer.

Parent–offspring regressions were used to test for heritable genetic variation in both body size and claw morphology. For each family ($n = 50$), mid-parent body size was regressed against the mean male progeny body size. The thumb length of the father's claws was regressed against the mean thumb length of the male progeny because siblings are not statistically independent. Families that produced only one male offspring were not included in the heritability estimates of claw morphology. Logistic regression was also used to test for the heritability of morph identity. Where significant heritabilities were detected (i.e. a significant regression), heritability coefficients were estimated as twice the slope of the parent–offspring regression lines (Falconer 1960).

(b) *Experimental manipulations*

(i) *Food quantity*

Two different food-level treatments were used to test for familial and food-quantity effects on the maturation times and male morph determination. The broods of 10 randomly chosen gravid field-caught females were each split, and 10 offspring were assigned to both the high- and low-quantity food treatments. Newly emerged juveniles were reared individually to maturity.

Juveniles in the low-quantity food treatment were fed 2×10^5 cells ml^{-1}, and those in the high-quantity treatment 4×10^5 cells ml^{-1} of the mixed algal diet described in § 2a without the addition of *Artemia* nauplii (a total volume of 25 ml in each tube). Juveniles were checked daily and the developmental rates were measured by the presence of exuviae (molted exoskeletons). At sexual maturity, the sex, male-morph identity, number of molts and time to maturation were recorded for each offspring ($n = 200$). The data were analysed in a two-way nested mixed-model ANOVA; the maturation time and number of molts to maturity were analysed separately. As the normality and homogeneity of the variance assumptions were violated and transformations were not always successful, the data were also analysed with non-parametric Wilcoxon two-sample tests or Kruskal–Wallis tests.

(ii) *Food quality*

The direct effects of diet quality, as well as the potential indirect effects of the mothers' diet (i.e. maternal effects) on morph determination and offspring developmental rates were studied under a low- and high-quality diet. The high-quality diet consisted of a mixture of five phytoplankton species: *D. tertiolecta*, *I. galbana*, *T. pseudonana*, *T. weissflogii* and *Cylindrotheca fusiformis* (a larger diatom species) plus rotifers (*Brachionus plicatilis*, *ca.* 500 rotifers per beaker). Rotifers are smaller than *Artemia* nauplii and therefore could be eaten by newly released juvenile amphipods. The low-quality diet lacked both diatoms and rotifers (an important source of proteins and fatty acids; Jonasdottir *et al.* 1995), and consisted of only two phytoplankton species, *D. tertiolecta* and *I. galbana*. Food quantity was not limited under either diet; amphipods on both diets were fed 250 ml of phytoplankton cells at 6×10^5 cells ml^{-1}.

Newly emerged juveniles drawn from a pool of over 500 offspring collected from 100 individual mating pairs of field-caught animals were assigned randomly to one of two food-quality treatments. These juveniles, which served as the maternal generation, were reared at a density of 10 individuals per beaker for each food-quality treatment ($n = 13$ replicate beakers for each food treatment). The time to maturity and proportion of major morphs were recorded.

Mature males and females within each treatment were pooled and group mated. The offspring from each of the two maternal diet-quality treatments were then split and randomly assigned to either the high- or low-quality food treatments. That is, progeny from the maternal group that experienced the low-quality food treatment were split into a low- ($n = 10$) and a high- ($n = 10$) quality food treatment, as were the progeny from the high-quality food maternal group. As before, juveniles were reared at a density of 10 individuals per beaker and the proportion of majors produced and maturation times were recorded. The data were analysed in a two-way ANOVA with maternal diet and offspring diet as the independent variables.

3. RESULTS

Regression of the mean progeny thumb length ($r^2 = 0.006$, $n = 46$; figure 2) and body size ($r^2 = 0.029$, $n = 46$) on paternal and mid-parent values, respectively, indicated that the morphological dimorphism was not heritable ($p > 0.05$). Similarly, logistic regression of morph identity on father's thumb length ($U = 0.0002$, $\chi^2 = 0.10$, $n = 339$) failed to detect a heritable component for morph determination ($p > 0.05$).

Developmental rates differed significantly between low- and high-quantity food treatments (table 1*a*). Juveniles raised on the high-quantity food treatment, as well as quality, matured significantly faster and with fewer molts than those fed the low-quantity food treatment (figure 3). Major males always took significantly longer than minors to develop, irrespective of diet (figure 3). Food quality ($F = 121.448$, $p < 0.0001$), unlike food quantity (Wilcoxon two-sample test, $U = 0.2140$, $p = 0.64$), also significantly affected morph determination—the development of major males was essentially limited to the high-quality diet (figure 4). These effects were consistent irrespective of the maternal diet, which significantly affected offspring maturation times (table 1*b*), but not morph determination.

4. DISCUSSION

(a) *Proximate basis for morph determination*

Both the experimental manipulations and quantitative genetic analyses indicate that the alternative male reproductive tactics in *Jassa* are conditional, with diet quality being the proximate environmental trigger. This mechanism is corroborated by seasonal shifts in the relative proportions of the male morphs (figure 5). Major morphs predominate during June and July and would have been born during the peak spring (March and April) phytoplankton bloom (Kurdziel 1999) when protein and fatty acid rich diatoms and nauplii are a major component of the plankton community (Lonsdale *et al.* 1996). Therefore these juvenile males would have experienced a 'high-quality' diet during their development.

Similar environmentally induced switch mechanisms (West-Eberhard 1989; Moran 1992; Roff 1996) have been documented in many other organisms, especially insects. In these cases, morph determination reflects changes in hormone levels that are affected by environmental conditions. For example, the effects of diet quality on morph determination in dung beetles, *Onthophagus taurus*, appear to be mediated by juvenile hormone titres (Emlen & Nijhout 1999). In at least two crustaceans (*Macrobranchium rosengergii* and *Libinia emarginata*), levels of methyl farnesoate, a juvenile hormone analogue, vary among male morphotypes (distinct ontogenetic stages) (Ra'anan & Sagi 1985; Laufer & Ahl 1995). Whether juvenile hormone (or an analogue) plays a role in morph determination in *J. marmorata* remains to be determined.

Figure 1. Contrasts between dimorphic males when compared with a female amphipod.

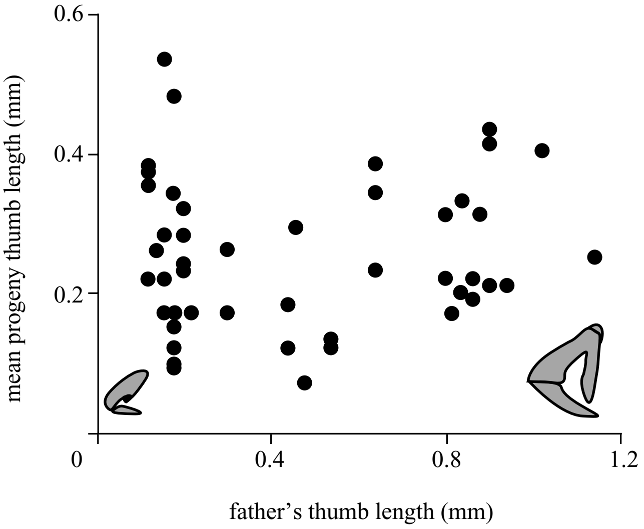

Figure 2. Regression of progeny thumb length on paternal thumb length ($n = 46$ families, $b = 0.026$, $r^2 = 0.006$, $p = 0.607$).

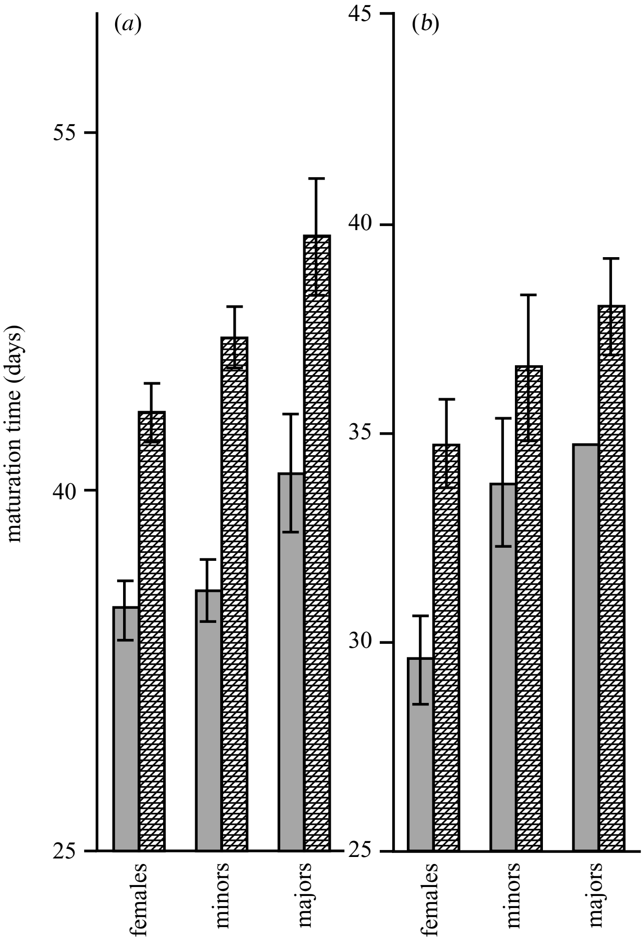

Figure 3. Comparison of developmental times among male morphs and females, as well as the consistent effect of both diet (*a*) quantity and (*b*) quality on maturation rates. Shaded area, high-quantity (*a*) or high-quality (*b*) food treatments; stipplied area, low-quantity (*a*) or low-quality (*b*) food treatments.

Unlike the case of coho salmon, *Oncorhynchus kisutch*, (Gross 1985, 1996), growth rates *per se* do not appear to determine alternative male tactics in *Jassa*. Although the absolute amount of time and number of molts is higher for the morphologically more elaborate and larger fighter males, compared with the minor males, the morphs share a common growth trajectory (i.e. a rate of 6.3 versus 5.99 days per molt for minors and majors, respectively). Thus, the growth trajectory in minors is truncated relative to majors, indicating that the physiological mechanism underlying morph determination in *Jassa* involves a heterochronic shift in the onset of maturation (e.g. Gould 1977; Alberch *et al.* 1979). While other amphipod genera in the family Ischyroceridae do not exhibit male dimorphisms, they are sexually dimorphic, in general. Males tend to be the larger sex and possess greatly exaggerated claws (i.e. gnathopods) (Conlan 1989). Geometric morphometric analyses confirm that minor *Jassa* males are paedomorphic, resembling juveniles more closely than majors (Kurdziel 1999). The production of minor males in *J. marmorata* would therefore appear to be a derived condition, and thus, the paedomorphic phenotype results from acceleration in the timing of maturation.

(**b**) *Implications for the evolution of alternative male reproductive tactics*

Conditional strategies may or may not be adaptive (e.g. Eberhard 1982; Gross 1996). To understand why and how selection favours alternative phenotypes, conditional strategies are often modelled using game theory and associated concepts such as the evolutionarily stable strategy (ESS) (Maynard Smith 1982). Due to the fact that social interactions can affect the fitness of an individual, they are commonly viewed as the force driving the evolution of alternative reproductive strategies and tactics (e.g. West-Eberhard 1989; Clark & Morjan 2001), especially with regards to the prevalent fighting and sneaking mating tactics that depend on body size (e.g. Gross 1985; Shuster & Wade 1991; Ryan *et al.* 1992; Emlen 1994). Ecology and demography may also play a role, but only to the extent that they influence the pay-offs or fitness functions of the alternative tactics, which are still defined by the selective pressures generated in the context of social interactions. For example, if an increase in population density causes greater interference for one morph relative to the other,

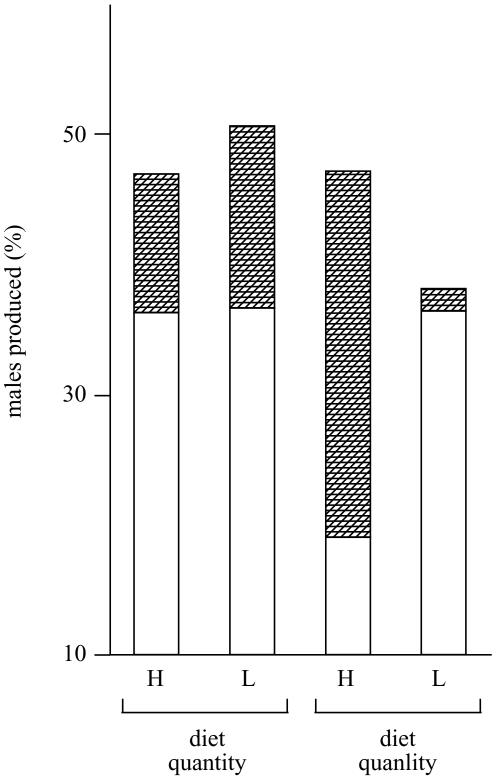

Figure 4. Contrasts between the effect of diet quality and quantity on male-morph determination. Only one major was produced on the low-quality diet. Stippled areas show majors. H, high; L, low.

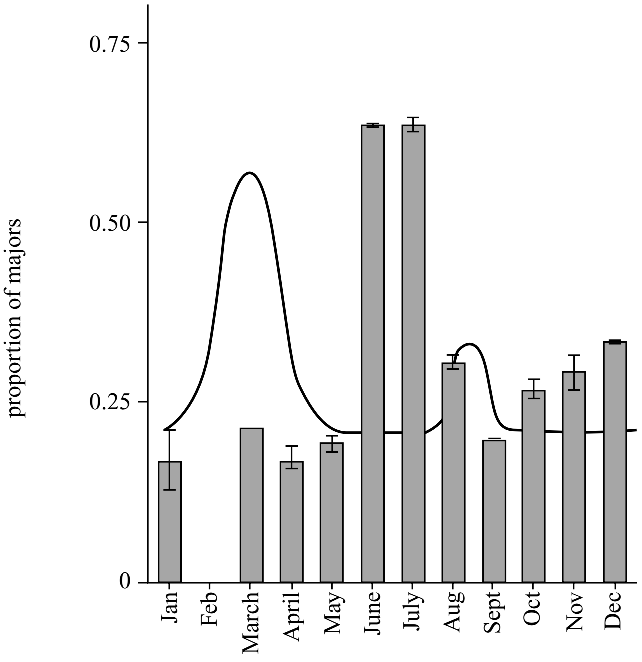

Figure 5. The seasonal shifts in the relative proportion of majors parallels changes in food availability (the general pattern of phytoplankton abundance is represented by the solid line). Data are means (± s.e.) based on monthly field samples over a two-year period.

perhaps because they employ different tactics with regard to holding a territory, the ESS distribution of alternatives in the population would be affected (Gross 1996). With this perspective, the focus is clearly on the phenotypic expression of a tactic. That is, the behavioural, morphological and physiological traits that distinguish the morphs are posited to be under selection because of their contributions to an individual's fitness in social interactions.

The conditional strategy in *Jassa* is not inconsistent with this interpretation. However, there is an alternative explanation—the dimorphism was generated by ecological selection. As discussed, shifts in the relative proportions of morphs under different dietary conditions in the experiments correspond to seasonal shifts of plankton abundance and composition (Lonsdale *et al.* 1996), indicating that the cue or trigger for the switch is related to diet. However, environment can have dual influences, serving as the cue for the developmental switch, but also affecting the relative fitness of the resulting phenotypic alternatives (e.g. Moran 1992). Not only would the social context that these animals experience differ dramatically because of extreme environmental shifts, but so would ecological selective pressures, such as those associated with the timing of reproduction. If maturation times are sufficiently influenced by varying environmental conditions, then ecological selection on such life-history traits could preclude a single male phenotype (Moran 1992; Roff 1996).

Distinguishing between these different selective pressures is not a trivial task because they can result in a common phenotype. Furthermore, they are certainly not mutually exclusive, and the social environment most likely is involved in the coupling of morphological and behavioural traits (e.g. Moczek & Emlen 1999), such as the sneaking behaviour of minor *Jassa* males (Clark 1997; Kurdziel 1999). However, significant seasonal differences in body size (e.g. average of 7.0 versus 4.6 mm between minors in April and November, $p < 0.001$) indicate that male phenotypes are not just a function of the social environment, but are also significantly affected by ecological factors. Although the relative proportion of morphs varies seasonally and corresponds to differences in plankton abundance and composition, minors were always produced (figure 5). This observation would be expected if temporal and spatial environmental heterogeneity prevents fine tuning of the developmental trigger governing morph production (Moran 1992).

Until the fitness functions of majors and minors have been estimated, it is not possible to determine whether social interactions may contribute to the evolution of this conditional strategy in *Jassa*. Nevertheless, the data do support the hypothesis that ecological selective pressures could have generated the minor alternative reproductive tactic. Ascribing causal agents to the evolution of a conditional strategy based solely upon phenotypic manifestations and the social environment that an expressed phenotype is likely to encounter, may be misleading. In *Jassa*, we have demonstrated that a simple heterochronic shift in maturation time results in the production of a paedomorphic or 'minor' phenotype. If, as we have indicated, this is an adaptive response to the immediate ecological environment (i.e. food resources), it would imply that the heterochronic process itself may be more fundamental to understanding the evolution of this conditional strategy than the phenotype itself (e.g. Gould 1977). Due to the fact that different heterochronic processes can result in similar manifestations, but occur under contrasting ecological selective pressures (e.g. paedomorphisms arising from accelerated maturation versus retarded somatic growth), processes that result in dimorphisms may provide a critical insight into questions of how and why alternative reproductive phenotypes evolve.

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