

Temporal allocation pattern between reproduction and growth within a breeding season of the hermit crab *Pagurus nigrivittatus*

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Abstract.—Allocation of energy between reproduction and growth is a fundamental principle in life history theory. In a seasonal environment, animals with indeterminate growth are predicted to change their allocation between reproduction and growth according to the season. We examined the seasonal variation in the allocation to reproduction and growth within a breeding season in the hermit crab *Pagurus nigrivittatus*. Females of *P. nigrivittatus* produced smaller clutches during the early part of the reproductive period than later although the frequency of prenuptial molting was lower early in the period. We suggest that environmental factors, such as temperature, may affect the development rate of embryos, as well as the metabolism and surplus energy in females, which have consequences for seasonal variation in the energy allocation to reproduction and growth.

Introduction

Energetic allocation between reproduction and growth is a fundamental tenet in life history theory (Roff, 1992; Stearns, 1992). The reason for this is because growth and reproduction compete for a limited supply of energy. The allocation pattern is relatively simple in annual animals with determinate growth, because the two processes are sequential rather than competitive and the only decision to be made is when to switch from growth to reproduction. However,

when perennial animals show indeterminate growth, they must optimize the use of resources to growth, or to reproduction, or to some combination of the two demands (Heino & Kaitala, 1999). In a seasonal environment, where abiotic and biotic conditions vary during a year, animals with indeterminate growth can partition energy between reproduction and growth according to season.

Females of some *Pagurus* hermit crabs, such as *P. filholi*, *P. minutus* and *P. nigrivittatus*, are considered to allocate energy to both reproduction and growth during a breeding season (Wada *et al.*, 2007, 2008). Females of these species have multiple clutches during each breeding season (Wada *et al.*, 2005), copulate before producing every clutch, and sometimes perform molting immediately prior to the copulation, which has been named as a prenuptial molt (Wada *et al.*, 2007). Males of *Pagurus* hermit crabs show precopulatory guarding behavior in which males grasp the aperture of the shell occupied by a mature female with their left chela for a period of up to several days (Hazlett, 1972, 1975; Wada *et al.*, 1995, 1996, 1999). By examining the pleopods of guarded females, the breeding continuity between clutches can be divided into two types; continuous and discontinuous breeding (Wada *et al.*, 2007, 2008; see Materials and Methods). Although females can grow larger with the prenuptial molt in *P. minutus* (Wada *et al.*, 2007) and *P. nigrivittatus* (Wada *et al.*, 2008), the frequency of prenuptial molts increases when females have discontinuous breeding. Thus, females that