

# Resource-dependent reproductive adjustment and the stability of consumer-resource dynamics

Takefumi Nakazawa · Takayuki Ohgushi ·  
Norio Yamamura

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**Abstract** This study explored a consumer-resource model including reproductive and nonreproductive subpopulations of the consumer to consider whether resource-dependent reproductive adjustment by the consumer would stabilize consumer-resource dynamics. The model assumed that decreasing (increasing) resource availability caused reproductive suppression (facilitation), and that the reproductive consumer had a higher mortality rate than the nonreproductive one (i.e., a trade-off between reproduction and survival). The model predicted that the variability would be reduced when the consumer had a strong tendency to suppress reproduction in response to low resource availability or when the cost of reproduction was high, although consumer extinction became more likely. Furthermore, when the consumer-resource dynamics converged to limit cycles, reproductive adjustment enhanced the long-term average of the consumer density. It was also predicted that if reproductive suppression enhanced resource consumption efficiency (i.e., a trade-off between reproduction and foraging), then it would destabilize the system by canceling the stabilizing effect of the reproductive adjustment itself. These results suggest that it is necessary not only to identify the costs of reproduction, but also to quantify the changes in individual-level performances due to reproduction in order to understand the ecological consequences of reproductive adjustment.

**Keywords** Breeding suppression · Phenotypic plasticity · Population cycle · Prey–predator interaction · Reproductive strategy

## Introduction

Reproduction is a key life-history component that influences demography directly, as well as foraging and defense (Clutton-Brock 1988). Undoubtedly, reproduction has some costs such as reduced parental survival (reviewed by Reznick 1985, 1992; Stearns 1992; Harshman and Zera 2006), and the degree of the trade-off depends on environmental factors, such as predation risk (see below) or resource availability (Zera and Harshman 2001; note here that “resource” represents “food” in this study unless stated otherwise, because we will explore consumer-resource models below). Therefore, reproductive adjustment can evolve in terms of mating frequency, offspring number, or feeding effort in a temporally changing environment. Indeed, resource-dependent reproductive adjustment occurs in many taxa, including zooplankton (Pond et al. 1996; Gyllström and Hansson 2004), insects (Moehrli and Juliano 1998; Kagata and Ohgushi 2001; Engqvist and Sauer 2003; Marden et al. 2003), fishes (Reznick and Yang 1993; Siems and Sikes 1998; Kolluru and Grether 2004), reptiles (Ford and Seigel 1989; Naulleau and Bonnet 1996; Shine and Madsen 1997; Doughty and Shine 1998; Madsen and Shine 1999; Du 2006), birds (Jacobsen et al. 1995; Erikstad et al. 1998; Meijer and Drent 1999; De Neve et al. 2004; Nagy and Holmes 2005), and mammals (Clutton-Brock et al. 1982; Saitoh 1989; Festa-Bianchet and Jorgenson 1998).

Recently, it has been argued that phenotypic plasticity could have a large impact on population or community

T. Nakazawa (✉) · T. Ohgushi  
Center for Ecological Research, Kyoto University,  
509-3, 2-chome, Hirano, Otsu, Shiga 520-2113, Japan  
e-mail: nkzw@ecology.kyoto-u.ac.jp

N. Yamamura  
Research Institute for Humanity and Nature, 457-4 Motoyama,  
Kamigamo, Kita-ku, Kyoto 603-8047, Japan

dynamics (reviewed by Schmitz et al. 2003; Werner and Peacor 2003; Miner et al. 2005; Ohgushi 2005; Young et al. 2006; Ohgushi et al. 2007). This view has been widespread especially among theoretical researchers (reviewed by Abrams 2000; Bolker et al. 2003). However, little is known about the ecological consequences of resource-dependent reproductive adjustment despite the accumulating empirical evidence (see above), although only a few empirical studies indicated the stabilizing effect (see “Discussion”). This is because previous theoretical studies have considered mainly foraging or defense adaptations (Abrams 2000; Werner and Peacor 2003).

On the other hand, predator-induced reproductive suppression in voles is one of the well-studied examples linking reproductive adjustment and population dynamics (e.g., Ylönen 1994; Norrdahl and Korpimäki 1995; Kokko and Ranta 1996). Ruxton and Lima (1997) and Ruxton et al. (2002) explored prey–predator models including reproductive and nonreproductive subpopulations of the prey (i.e., voles). In the model, they assumed that reproductive prey suffered a higher predation rate than nonreproductive prey (i.e., a trade-off between reproduction and predator avoidance), and that increasing (decreasing) predator density enhanced behavioral switching from the reproductive (nonreproductive) into the nonreproductive (reproductive) stage. Gyllenberg et al. (1996) also worked on the same problem by exploring more specific models. In general, these models predict that predator-induced reproductive adjustment tends to be stabilizing, because reproductive suppression (facilitation) reduces (enhances) the population growth rate of the predator when the predator is abundant (scarce), which causes a negative feedback in the prey–predator dynamics (but see also Ylönen 1994).

Furthermore, Kokko and Ruxton (2000) explored a prey–predator model that included reproductive adjustment by both the prey and predator. However, because of the complexity of their model structure, we only know that the influences of reproductive adjustment on population stability would be complicated (see “Discussion” for further explanations). Therefore, more generalized and simple mathematical models are required to understand population dynamics in which reproductive behaviors change flexibly in response to resource availability.

In this study, we model the situation that increasing (decreasing) resource density enhances behavioral switching of the consumer from the reproductive (nonreproductive) into the nonreproductive (reproductive) stage, to examine whether resource-dependent reproductive adjustment would stabilize the consumer–resource dynamics. Although reproductive adjustment observed in nature is not necessarily a switching behavior, but rather a quantitative trait in many cases, we follow Ruxton and Lima (1997) and Ruxton et al.

(2002) who assumed reproductive and nonreproductive subpopulations of prey (i.e., resource) but not of predator (i.e., consumer).

Furthermore, as cost of reproduction, we assume that the reproductive consumer has a higher mortality rate than the nonreproductive one, for example, because of energetic constraints (see above) or increased vulnerability to predation (Gwynne 1989) or parasitism (Sheldon and Verhulst 1996). These assumptions imply a trade-off between reproduction and survival, which is the most conventional trade-off (Reznick 1985; Stearns 1992). Although organisms in nature suffer from higher mortality and die from starvation when the resource availability is extremely low, we do not consider the extreme case for the purpose of highlighting potential demographic effects of resource-dependent reproductive adjustment (but see also “Discussion” for expected results). In addition, a decrease in foraging effort has also been reported as a cost of reproduction in many cases (e.g., Shine 1980; Oksanen and Lundberg 1995; Kolluru and Grether 2004; Nagy and Holmes 2005), which will also affect demographic effects of resource-dependent reproductive adjustment. Thus, we also consider the situation that the reproductive consumer has lower resource consumption efficiency than the nonreproductive one. We also discuss the support that our model predictions would provide for empirical studies.

## Model

The model simply assumes that decreasing (increasing) resource availability causes reproductive suppression (facilitation) of the consumer, and that the reproductive consumer has a higher mortality rate than the nonreproductive one (i.e., a trade-off between reproduction and survival). These assumptions do not rigorously maximize consumer fitness, but the behavior will be adaptive to some degree, as suggested in previous empirical (see “Introduction”) and theoretical studies (Gyllenberg et al. 1996; Ruxton and Lima 1997; Ruxton et al. 2002).

In the model, we consider one resource ( $R$ ) and two subpopulations of consumer, reproductive ( $B$ ) and nonreproductive ( $S$ ), in a consumer–resource model.

$$\frac{dR}{dt} = r \left( 1 - \frac{R}{K} \right) R - F(R)(B + S) \quad (1a)$$

$$\frac{dB}{dt} = bF(R)B - P(F)B + Q(F)S - d_B B \quad (1b)$$

$$\frac{dS}{dt} = P(F)B - Q(F)S - d_S S \quad (1c)$$

where

$$F(R) = \frac{aR}{1 + haR}. \tag{1d}$$

$r$  and  $K$  are the intrinsic growth rate and the carrying capacity of the resource ( $R$ ), respectively. The functional response  $F$  is Holling’s type II (Eq. 1d), in which  $a$  and  $h$  represent the maximum resource consumption rate and the handling time, respectively.  $b$  is the conversion efficiency of reproductive energy by the consumer.  $d_B$  and  $d_S$  are the mortality rates of the reproductive and nonreproductive consumers, respectively.  $P$  and  $Q$  capture the magnitudes of reproductive suppression and facilitation, which depend on the per-individual foraging gain  $F$  by assumption. In this study, following Ruxton and Lima (1997) and Ruxton et al. (2002), we set  $P$  and  $Q$  as decreasing and increasing saturating functions of  $F$ , respectively:

$$P(F) = \frac{p_0}{1 + p_1F(R)} \tag{1e}$$

$$Q(F) = \frac{q_0F(R)}{1 + q_1F(R)} \tag{1f}$$

These formulations assume that an increase in the foraging gain decreases (or increases) the per-individual switching rate from the reproductive into the nonreproductive stage (or vice versa). The maximum suppression and facilitation rates are governed by  $p_0$  and  $q_0$ , respectively.  $p_1$  and  $q_1$  determine the saturation speed. In this model, we assume  $d_B > d_S$ , which implies a cost of reproduction. Substituting  $d_B = c d_S$  ( $c > 1$ ), we denote the magnitude of the cost with  $c$ .

It is difficult to analyze the model, even to obtain the equilibrium density analytically. Accordingly, we analyze the properties of the system numerically by using computer simulations. Here, we first calculate the equilibrium densities numerically and then examine local stability from the Routh-Hurwitz criteria on the Jacobian matrix resulting from the linearization process. We examine parameter-dependences of local stability of the equilibria and conduct those procedures for different initial conditions to test whether bistability or chaotic dynamics exist. Furthermore, we also examine the long-term average of the total consumer density (i.e.,  $B + S$ ). This evaluation will be helpful to consider the adaptive significance of reproductive adjustment, although it does not rigorously indicate consumer fitness.

When the consumer changes the maximum resource consumption rate  $a$  due to reproductive suppression, the rate of resource increase (Eq. 1a) would be rewritten as follows:

$$\frac{dR}{dt} = r \left( 1 - \frac{R}{K} \right) R - F(R)B - F(zR)S \tag{2}$$

where  $z$  represents the magnitude of the change in the resource consumption rate. In this case, we also conduct similar numerical simulations to examine demographic effects of reproductive adjustment.

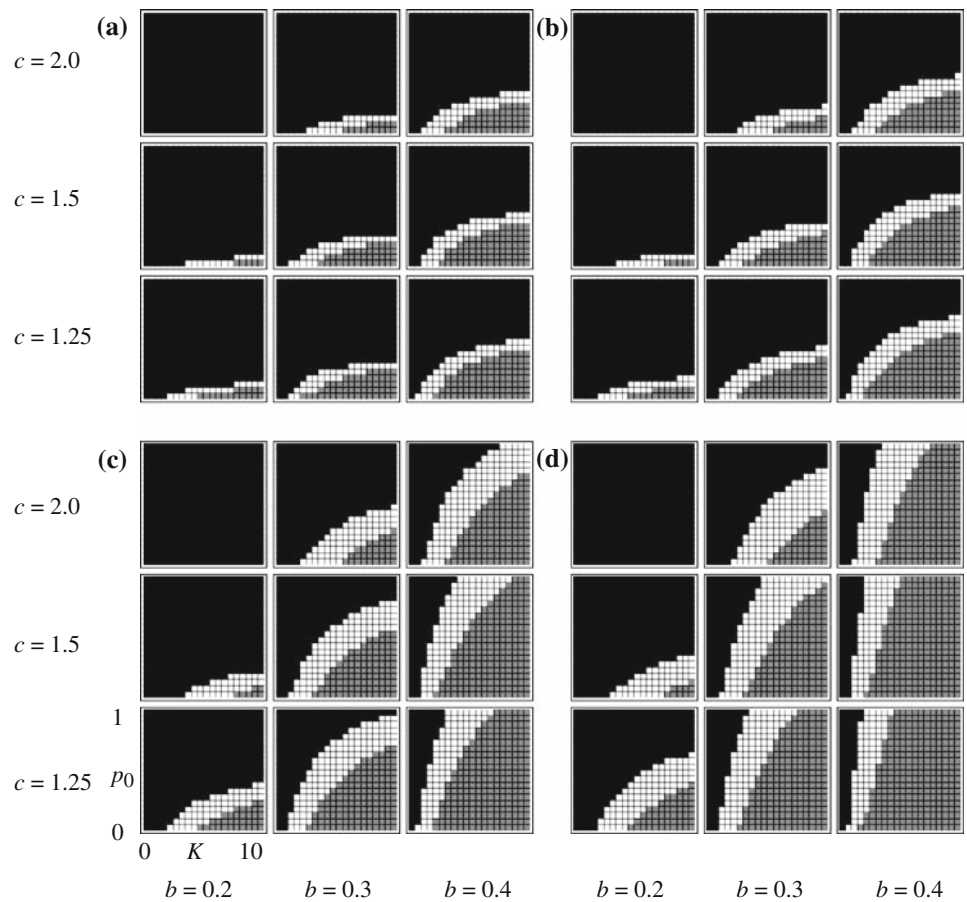
### Results

Figure 1 shows the dependence of local stability of the equilibria on several parameters ( $K, p_0, q_0, b, c$ ). The model always predicted three types of dynamics: consumer extinction (black regions), coexistence equilibrium (white regions) and limit cycle coexistence (gray regions). It was unlikely that bistability existed, because the results did not change with the initial conditions. That is, when locally stable, the dynamics were always globally stable and when locally unstable, they approached limit cycles.

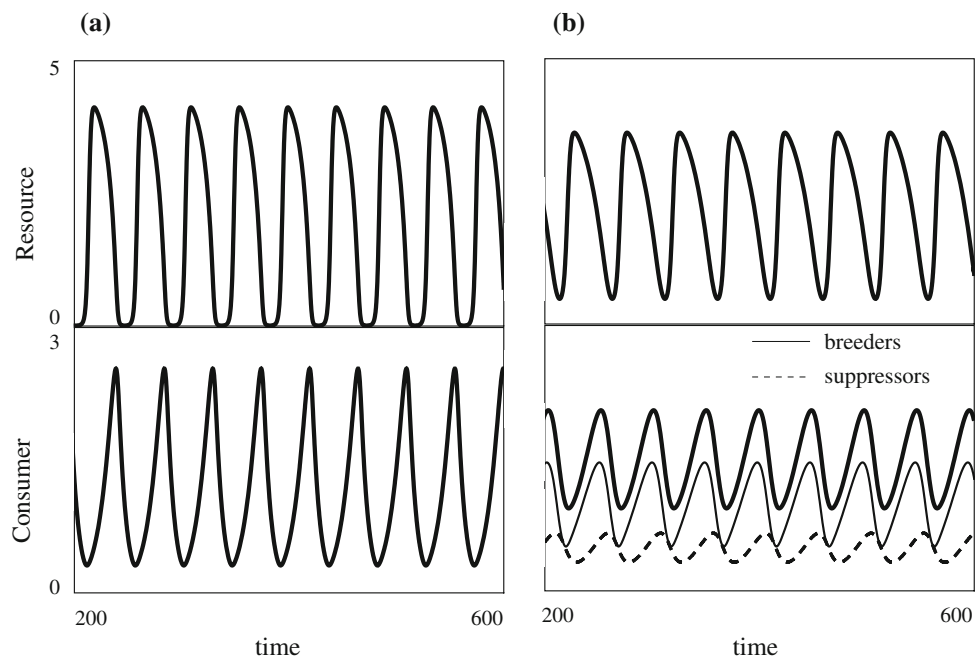
We found that the dynamic property at the equilibrium state would change from limit cycle coexistence (gray region) to consumer extinction (black region) via stable coexistence (white regions) with increasing maximum reproductive suppression rate  $p_0$  or mortality cost of reproduction  $c$  and decreasing carrying capacity of the resource  $K$ , conversion efficiency of the reproductive energy  $b$  or maximum reproductive facilitation rate  $q_0$  (Fig. 1). Large values of  $p_0$  and small values of  $q_0$  mean that the consumer has a strong tendency to suppress reproduction in response to resource deficiency. Small values of  $b$  and large values of  $c$  mean that the relative mortality cost of reproduction is high. Therefore, the obtained patterns in Fig. 1 will be explained by a well-known fact in consumer-resource interactions: if the population growth rate of the consumer is reduced, then the equilibrium resource density increases and the dynamics become more stable (Murdoch et al. 2003).

From Fig. 1, it can be inferred that reproductive adjustment reduces the variability (i.e., the amplitude of the population oscillations) of the consumer-resource dynamics, if they coexist. Figure 2 shows examples of the dynamics of resource and consumer densities without and with reproductive adjustment, illustrating the stabilizing effect of reproductive adjustment on population dynamics (i.e., reducing the variability) when it is not strong enough to stabilize the coexistence equilibrium. In both numerical simulations, the initial conditions were  $R(0) = K$  and  $B(0) = S(0) = 0.01$ . It is also notable that the variability of the system will be always reduced when the consumer has the capability to suppress reproduction ( $p_0 > 0$ ) compared to when the consumer does not ( $p_0 = 0$ ; Fig. 1), although the consumer did not persist when the parameter change was sufficiently large (black regions; Fig. 1).

**Fig. 1** Parameter-dependence of the local stability of the equilibria for  $q_0 = \mathbf{a}$  0.01,  $\mathbf{b}$  0.1,  $\mathbf{c}$  0.5, and  $\mathbf{d}$  1.0. In each small panel, the *horizontal* and *vertical axes* represent the carrying capacity of the resource and the maximum reproductive suppression rate ( $K$  and  $p_0$ ), respectively. Panels are arranged in order of the reproductive conversion efficiency ( $b = 0.2, 0.3$ , and  $0.4$ ) and the magnitude of the mortality cost of reproduction ( $c = 1.25, 1.5$ , and  $2$ ). In the *black* area, the trivial equilibrium is locally stable (consumer extinction). The *white* and *gray* areas represent the regions in which the internal equilibrium converges to coexistence equilibrium and limit cycles, respectively. Other parameter values are set as  $r = 1, a = 1, h = 1, d_s = 0.1, p_1 = 1$ , and  $q_1 = 1$

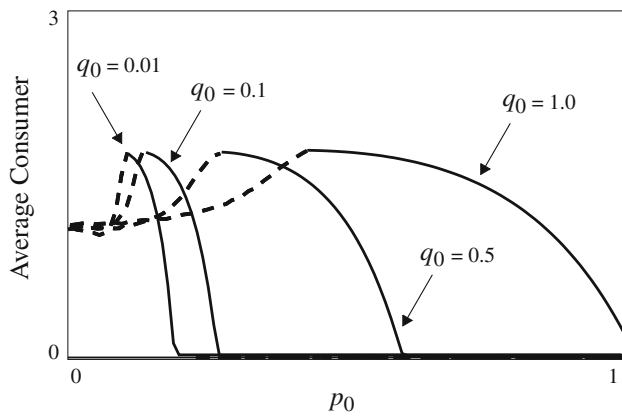


**Fig. 2** Dynamics of resource and consumer densities **a** without and **b** with reproductive adjustment (*bold lines*).  $p_0 = \mathbf{a}$  0 and  $\mathbf{b}$  0.11;  $K = 5, b = 0.3, c = 1.5$ , and  $q_0 = 0.1$ . Other parameter values are the same as in Fig. 1. The *solid line* denotes breeders; the *broken line* denotes suppressors



Qualitatively similar patterns were obtained for different parameter settings of  $(r, a, h, d_s, p_1, q_1)$  (not shown). Additionally, we observed that decreasing intrinsic growth

rates of the resource  $r$  or increasing mortality rates of the nonreproductive consumer  $d_s$  enhanced the stabilizing effect of reproductive adjustment on the variability of the



**Fig. 3** Long-term average of total consumer density  $B + S$  for various values of the reproductive facilitation rates ( $q_0 = 0.01, 0.1, 0.5,$  and  $1.0$ ). The  $x$  axis represents the reproductive suppression rate  $p_0$ . Other parameter values are the same as in Fig. 2. The *solid* and *broken lines* denote that the dynamics converge to coexistence equilibrium and limit cycles, respectively

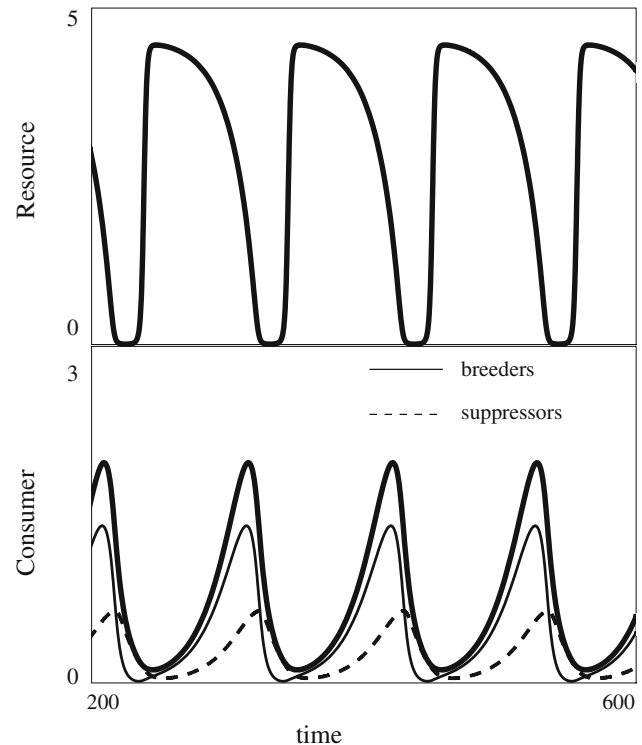
consumer-resource dynamics (not shown). These results agree with the predictions in general consumer-resource models (Murdoch et al. 2003).

Figure 3 shows how the reproductive suppression rate  $p_0$  would affect the long-term average of the total consumer density (i.e.,  $B + S$ ) for various values of the reproductive facilitation rates  $q_0$ . We obtained qualitatively similar patterns, where the time-averaged consumer density increased (decreased) when the consumer-resource dynamics converged to limit cycles (coexistence equilibrium) as  $p_0$  increased.

Finally, we found that, if the reproductive consumer has a lower resource consumption efficiency (Eq. 2), the variability was slightly augmented (compare Figs. 2b and 4), although the stability condition was almost invariant (not shown).

### Discussion

In this study, we examined how resource-dependent (i.e., food-dependent) reproductive adjustment by the consumer would affect the consumer-resource dynamics. Previous theoretical models have also described reproductive plasticity in community ecological contexts (e.g., size-structured models; de Roos 1997). In those models, dynamic properties of populations were modified by plastic changes in interaction strength between consumer and resource (e.g., due to size-dependent consumption efficiency). In our models, however, the population growth rate of the consumer changed internally due to plasticity in reproductive efforts, which influenced the whole system through the interspecific interaction with constant strength.



**Fig. 4** Dynamics of resource and consumer densities when reproductive suppression enhances the resource consumption efficiency.  $z = 2$  and  $p_0 = 0.11$ . Other parameter values are the same as in Fig. 2

We showed that resource-dependent reproductive adjustment would basically stabilize (i.e., reduce the variability of) the consumer-resource dynamics under a trade-off between reproduction and survival. In standard consumer-resource models (i.e., the Rosenzweig–MacArthur model; Rosenzweig and MacArthur 1963), the consumer population grows by exploiting the resource and starts to decrease when the resource density declines to a certain level. Subsequently, the resource begins to recover as the consumer population decreases (Fig. 2a). With reproductive adjustment, however, the resource is not depleted to such a low level because the consumer reduces reproductive investment and the population decreases earlier when the resource is scarce (Fig. 2b). Moreover, when the resource is abundant, the consumer invests more in reproduction and the population increases more quickly, which enhances resource consumption. As a result, these effects reduced the variability. On the other hand, reproductive adjustment was predicted to be destabilizing (i.e., enhance the variability) under a trade-off between reproduction and foraging. This destabilization effect will be attributable to the fact that the resource is consumed (grows) excessively due to an increase in the nonreproductive (reproductive) consumer with high (low) consumption efficiency when the resource is scarce (abundant).



A number of studies have shown that the costs of reproduction are resource-dependent and that parents adjust their reproductive investment based on resource availability (see “Introduction”). Although researchers have considered the ecological consequences of reproductive adjustment less often, there is some empirical evidence that agrees with our model predictions on the variability of population dynamics. For example, an herbivorous ladybird beetle *Epilachna niponica* shows egg resorption in response to increased herbivory, allowing it to overwinter and survive to the next reproductive season in the natural habitat (Ohgushi 1996). When the ladybird was introduced to a site with different host plant phenology, the introduced population shifted to early reproduction at the cost of reduced longevity, and as a result, egg resorption no longer occurred (Ohgushi 1991, 1998; Ohgushi and Sawada 1997a). Comparing the temporal dynamics of the source and introduced populations, it was found that the introduced population exhibited more variable dynamics (Ohgushi and Sawada 1997b, 1998; Ohgushi 1998), suggesting that egg resorption greatly contributed to stabilization of the ladybird population (Ohgushi and Sawada 1985, 1998; Ohgushi 1998). These results indicate a stabilizing effect of resource-dependent reproductive adjustment directly.

Another example is resting-egg production by zooplankton. Many zooplankton species produce resting (dormant) eggs in response to certain environmental changes, such as food deficiency (reviewed by Gyllström and Hansson 2004). Resting eggs stay at the bottom of a lake until the environment improves, and thus do not contribute to instantaneous population growth. Accordingly, nonresting individuals and resting eggs can be regarded as the reproductive and nonreproductive subpopulations, respectively, in our model. Resting eggs have extremely low levels of both mortality and hatching rates (Hairston et al. 1995), which would correspond to a large value of reproductive cost  $c$  and a small value of reproductive facilitation rate  $q_0$ . Moreover, resting eggs do not consume food, so  $z = 0$ . Therefore, our results predict that resting-egg production would have a stabilizing effect on the population dynamics. Indeed, McCauley et al. (1999) observed that resting-egg production stabilized the population dynamics in algae-*Daphnia* microcosm experimental systems, which is being tested using mathematical models (T. Nakazawa et al., in preparation).

Previous theoretical studies have predicted that predator-induced reproductive suppression of prey would stabilize the prey-predator dynamics (Gyllenberg et al. 1996; Ruxton and Lima 1997; see also Ylönen 1994; Ruxton et al. 2002). Therefore, together with our predictions, it is expected that if both prey and predator (i.e., resource and consumer) adjust their reproductive

investment based on the density of the other, the system should be more stable. Conversely, Kokko and Ruxton (2000) argued that the ecological consequences of reproductive adjustment would be more complicated, explaining that reproductive adjustment either stabilized or destabilized the system and there seemed to be no simple general rule governing the effects.

To date, few arguments have been made about this inconsistency among the predictions of these previous models. One big difference between the assumptions of the models concerns the optimization process of reproductive investment. Ruxton and Lima (1997) and Ruxton et al. (2002) assumed a priori that the switching rates between the reproductive and nonreproductive subpopulations were determined by predator and prey densities, while Kokko and Ruxton (2000) optimized the reproductive investment to maximize fitness, which was defined as the sum of parental survival and offspring recruitment. However, we consider that a more important factor is the difference in stage-specific performances. For example, suppose that the juvenile generally has lower resource consumption efficiency than the adult, as Kokko and Ruxton (2000) assumed. When adults increase their reproductive investment in response to increasing resource availability, the adults suffer a higher mortality rate due to the cost of reproduction, which potentially has a destabilizing effect because a reduction in the consumer population facilitates overgrowth of the resource. Meanwhile, the increased reproductive investment may not enhance resource consumption, even with juvenile recruitment, if the consumption efficiency of the juvenile is very low. Consequently, reproductive adjustment can counterintuitively destabilize the system. Therefore, whether reproductive adjustment stabilizes or destabilizes the system will depend on the reproductive output, a cost of reproduction, and the relative performances (e.g., resource consumption efficiency or mortality rate) of the adult and juvenile. This hypothesis is further extended by our prediction that if the consumer enhances the resource consumption efficiency due to reproductive suppression, it would destabilize the system by canceling the stabilizing effect of reproductive adjustment itself (Fig. 4). Therefore, to understand the ecological consequences of reproductive adjustment, it is necessary not only to identify the costs of reproduction, but also to quantify the changes in age- or behavior-dependent individual-level performances due to reproduction.

In this study, we showed that reproductive adjustment would be not only stabilizing but also advantageous (disadvantageous) to the consumer when the consumer-resource dynamics converge to limit cycles (coexistence equilibrium) (Fig. 3). These patterns are compatible with the prediction that when the functional response of the consumer is nonlinear, the large amplitude cycles generally

reduce the mean growth rate of the consumer (Abrams et al. 1997, 1998, 2003). We modeled reproductive adjustment by the consumer phenomenologically in the density-dependent way, without considering consumer fitness explicitly. Although there is still debate over the extent to which phenotypic plasticity is adaptive in behavioral ecology (Via et al. 2001; Pigliucci 2005; Ghalambor et al. 2007), it would also be interesting to see how model predictions would change by explicitly introducing optimal reproductive strategy, because it may be predicted to contribute to population stability.

We simply assumed an increasing mortality rate as a cost of reproduction. However, the cost may affect future performance (i.e., a time-delayed trade-off; Gustafsson and Sutherland 1988; Nilsson and Svensson 1996; Shine and Madsen 1997; Doughty and Shine 1998). In this case, it is necessary to model life-history optimization on a time scale shorter than the individual lifespan. A classic approach is to maximize the eigenvalue of the age-structured matrix model including life-history trade-offs (Caswell 1989). More recently, a state-dependent life-history model has been proposed in a dynamic optimization approach (e.g., Perrin and Sibly 1993; McNamara and Houston 1996). However, it is still difficult to apply these methods to community models that include the dynamics of other species (i.e., resource or predator). Therefore, we attempted to eliminate the influences of the time-delayed trade-off by assuming that life-history optimization would be achieved immediately on a long time scale in which the population dynamics reached the equilibrium state. More refined mathematical models are necessary for a rigorous investigation of how the population dynamics would be affected by life-history optimization under a time-delayed trade-off.

Furthermore, we also considered that the resource availability influenced only reproductive efforts of the consumer whereas other demographic parameters such as mortality rate were invariant. Therefore, our model is minimal in its structure, allowing us to highlight and investigate potential demographic effects of resource-dependent reproductive adjustment. However, the mortality rate, for example, of the consumer may increase with decreasing resource availability due to starvation. This assumption may reduce the stabilizing effect of reproductive adjustment because, when the resource availability is extremely low, a slight increase in the resource availability would enhance the population growth rate of the consumer considerably, which could rather exhaust the resource.

Finally, we would like to emphasize that phenotypic plasticity occurs in diverse reproductive traits: for example, in fish species, it has been reported that egg size (Reznick and Yang 1993), hatching date (Wedekind 2002), sex ratio (Römer and Beisenherz 1996), age at maturity (Stearns and Koella 1986), mating strategy (Klemetsen et al. 2003), and

sexual role (Munday et al. 2005) change plastically in response to environmental changes. Researchers have rarely tested whether or how phenotypic plasticity in these traits affects population or community dynamics. More consideration should be given to phenotypic plasticity in reproductive traits in community ecological studies in addition to foraging or defense plasticity, considering the increasing concern over a linkage between individual levels of trait plasticity and community dynamics (Schmitz et al. 2003; Werner and Peacor 2003; Miner et al. 2005; Ohgushi 2005; Young et al. 2006; Ohgushi et al. 2007). This will provide profound insights into our understanding of community dynamics in nature, as will emerging new study fields linking community ecology and evolutionary biology (Johnson and Stinchcombe 2007).

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