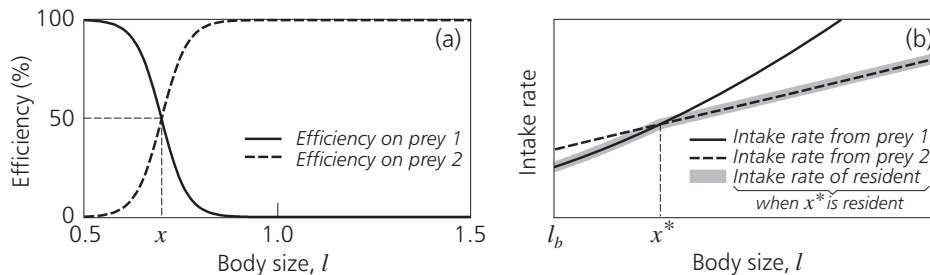**Box 10.3** Adaptive speciation through ontogenetic niche shifts

David Claessen and Ulf Dieckmann

This box introduces a simple mechanistic model to demonstrate how adaptive speciation in size-structured populations can result from the interplay between ontogenetic niche shifts (Werner and Gilliam 1984) and environmental feedback (Heino *et al.* 1997). Arctic char, for example, undergo an ontogenetic niche shift from benthivory to planktivory at body sizes of 10 to 17 cm (Snorrason *et al.* 1994a; Langeland and L'Abee-Lund 1998).

Motivated by this and other systems, the model (Claessen and Dieckmann 2002) is based on the assumption that individuals predominately exploit one type of prey (prey 1) while their body size l is small, $l < x$, and a second type of prey (prey 2) once they have grown to larger sizes, $l > x$. This niche shift is assumed to be irreversible and is determined by an individual's genotype x, referred to as its switch size.

Individuals are born at size l_b. Their intake rates follow a size-dependent type-II functional response, determined by handling times and attack rates (Mittelbach 1981; Persson and Greenberg 1990). Handling times decrease with body size according to an allometric function. Attack rates are modeled as the product of a maximum feasible attack rate, increasing allometrically with body size, and the sigmoidal efficiency functions depicted in panel (a). Allocation of ingested energy follows the κ-rule (Kooijman and Metz 1984): a fraction $1 - \kappa$ of the total energy intake is invested in reproduction; the remaining energy is used first to meet metabolic costs (proportional to body volume) and then to invest in somatic growth. As a result of mutation, there is a small possibility that the genotype of individual offspring will differ slightly from that of the parents. The two prey populations are unstructured and are described by semi-chemostat dynamics (Persson *et al.* 1998).
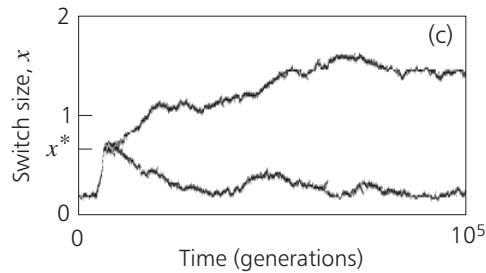
Environmental feedback arises from the impact of consumption on the density of the two prey populations. If the niche shift occurs at a very large switch size x, hardly any individuals survive to exploit the second niche. Prey 1 is then overexploited while prey 2 is underexploited. If, by contrast, the ontogenetic niche shift occurs very early in life, prey 1 is abundant whereas prey 2 is depleted.

Panel (c) shows a stochastic realization that corresponds to the latter situation. The population starts out from a switch size $x < l_b$ and thus essentially only

Box 10.3 *continued*

exploits prey 2, leaving prey 1 at high abundance. For the chosen parameter values, the switch size x^* is both convergence stable and evolutionarily unstable. As illustrated in the figure, this means that directional selection first brings an almost monomorphic population into the vicinity of this switch size; however, once x^* has been reached, selection turns disruptive and two different ecomorphs emerge.

The mechanism that underlies this somewhat counterintuitive process can be understood by considering panel (b). The size-dependent intake rates from the two prey types depend on their exploitation and thus on the switch size that is resident in the population. For a given resident, adopting the switch size at the intersection of these curves either maximizes or minimizes the total intake. When x^* is resident, the resultant intake rates intersect at $l = x^*$. Convergence toward x^* is driven by environmental feedback. Perturbing the resident switch size a little away from x^* explains how this works: a resident that shifts exploitation at a slightly smaller size, $x < x^*$, underexploits prey 1 and overexploits prey 2. This means that, in panel (b), the continuous curve for prey 1 moves down while the dashed curve for prey 2 moves up. If such a resident now gives rise to a mutant that shifts later, this mutant profits from prey 1 more than the resident itself; it can therefore invade. The opposite is true for perturbations with $x > x^*$. This ensures evolutionary convergence toward x^*.

By considering the fate of mutants in the environment set by the resident x^*, we can see that x^* is not evolutionarily stable. Compared to the resident, a mutant that switches at a smaller size profits more from an increased intake rate from prey 2 than it loses on prey 1. Conversely, a mutant that switches at a larger size profits more from an increased intake rate from prey 1 than it loses on prey 2. This shows that x^* is a fitness minimum and thus gives rise to disruptive selection. Since it is also convergence stable, x^* is an evolutionary branching point (Chapter 4). These conclusions are valid, if, as for panel (c), the intake rate increases faster with body size for prey 1 than for prey 2. In the opposite case, x^* is convergence stable and evolutionarily stable: no evolutionary branching is then expected.

To assess whether the eco-evolutionary mechanism proposed here can explain observed resource polymorphisms and the potentially ensuing processes of adaptive speciation, estimates of how intake rates in two alternative niches scale with body size will be of critical importance.