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A maladaptive intermediate form: a strong trade-off revealed by hybrids between two forms of a snail-feeding beetle

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Abstract. Although trade-off curves between fitness components are essential in theoretical studies of ecological specialization, few empirical studies have actually determined these curves experimentally. Using the snail-feeding carabid beetle *Damaster blaptoides*, which is endemic to the Japanese archipelago, we estimated the trade-off curve for feeding success with alternative foraging behaviors that are linked to varying morphology. First, we crossed a stout-bodied and a slender-bodied subspecies and produced their F_1 and backcross hybrids, which exhibited intermediate body shapes. Then we compared the snail-feeding success of these beetles. Stout beetles could eat small snails by crushing shells, whereas slender beetles could eat large snails by inserting their heads into shells. Although hybrids with intermediate body shapes attempted to employ both strategies, they frequently failed at both. The relationship between feeding success rate and beetle body shape was represented by an inward bending curve, which implies a strong trade-off that can cause disruptive selection, leading to ecological specialization. We suggest that the intermediately shaped beetles were maladapted for snail-feeding and that disruptive selection may have played an important role in the morphological divergence of these beetles.

Key words: adaptive radiation; disruptive selection; ecological specialization; generalist; morphological discontinuity; predator–prey interaction; specialist.

INTRODUCTION

The evolution of ecological specialization to specific niches has been a central topic in ecology and evolutionary biology (Futuyma and Moreno 1988), and is frequently indicated as an important component of adaptive radiation (Schluter 2000, Gavrilets and Losos 2009). A major controversial issue in studies of ecological specialization involves the verification of the trade-off principle (Fry 1996, Whitlock 1996). Although the idea of ecological specialization is supported by theoretical studies, most theoretical models are based on the assumption that a trade-off exists in niche use among specialized phenotypes (Wilson and Yoshimura 1994, Ravigné et al. 2009). For example, it is assumed that large predators capture large prey efficiently but small prey inefficiently, whereas small predators capture small prey efficiently but large prey inefficiently. Because of this negative correlation in ecological performances, divergence can occur between large and small predators as an evolutionary consequence of specialization (Rueffler et al. 2006*c*). However, few empirical studies have examined the validity of assumed trade-offs. The need for empirical studies was noted in the pivotal review of ecological specialization by Futuyma and Moreno (1988) more than two decades ago, in which they suggested that more physiological and functional morphological studies were needed to support the trade-off principle. A recent review by Forister et al. (2012) suggests that the empirical evidence of trade-offs remains insufficient.

The shape of a trade-off curve is the key to determining evolutionary consequences in theoretical models of specialization (Levins 1962, Rueffler et al. 2004). A trade-off curve involves a two-dimensional plot of fitness components that represent, for example, the feeding performances of large and small predators on large and small prey (Fig. 1A). A curve that bends outward (e.g., line (1) in Fig. 1A) implies that an increase in one fitness-component value weakly decreases the other among the set of feasible phenotypes. A trade-off represented by an outward bending curve is referred to as a “weak trade-off” (Rueffler et al. 2006*c*, Ravigné et al. 2009). In contrast, a curve that bends inward (e.g., lines (3) and (4) in Fig. 1A) implies that an increase in one fitness-component value causes a strong

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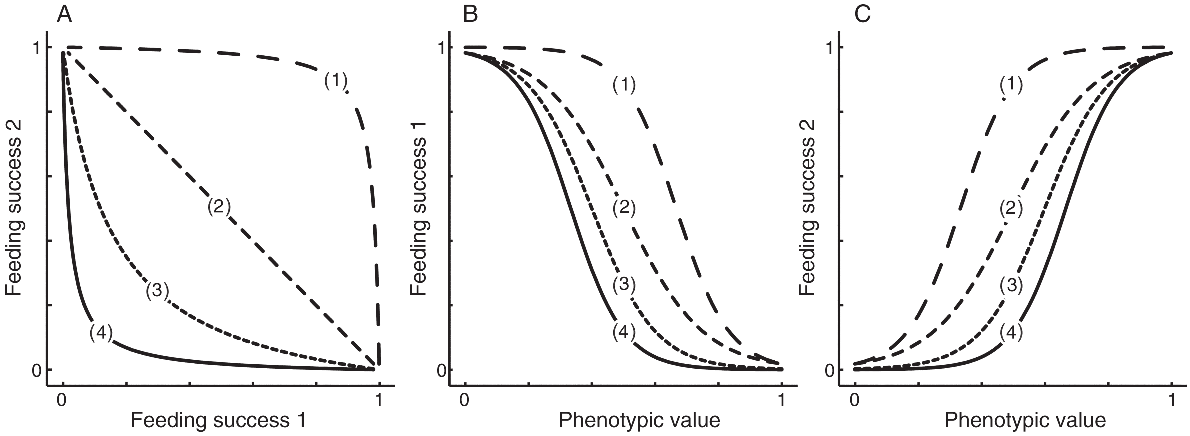

FIG. 1. (A) Trade-off curves. Fitness components on two-dimensional plots describe lines with negative slopes, which imply that increases in the performance of one factor cause decreases in the performance of the other. For example, large predators have high capture performance with large prey but low performance with small prey, and vice versa. Lines (3) and (4) indicate situations in which the effect of the trade-off is relatively strong. These lines were plotted using logistic functions (see *Methods*). Parameter values were: (1) $a_1 = -12$, $b_1 = 4$; (2) $a_1 = -8$, $b_1 = 4$; (3) $a_1 = -10$, $b_1 = 6$; (4) $a_1 = -12$, $b_1 = 8$. $a_2 = -a_1$ and $b_2 = a_1 + b_1$, where a_1, a_2, b_1, and b_2 are parameters that determine the shape of a trade-off curve. (B) Feeding success 1 and (C) feeding success 2 were plotted as logistic functions of phenotypic value x, using the same parameter sets for lines (1)–(4) as in panel (A).

decrease in the other; a trade-off represented by an inward-bending curve is referred to as a "strong trade-off." Because strong trade-offs play important roles in phenotypic diversification (Wilson and Yoshimura 1994, Ravigné et al. 2009), the clarification of trade-off curves is important in studies of character divergence (Benkman 1993, Schluter 1993, Hatfield and Schluter 1999), phenotypic plasticity (Parsons and Robinson 2007), and ecological specialization (Futuyma and Moreno 1988).

The snail-feeding performances of carabid beetles *Damaster blaptoides* exemplify a trade-off in functional morphology (Konuma and Chiba 2007). Stout-shaped beetles (with wide, short forebodies) can eat small snails by crushing shells because their bite is powerful. Slender beetles (with narrow, long-headed forebodies) cannot crush snail shells because their bite is weak, but they can eat snails by inserting their heads into shells and directly eating the snail's soft tissues. Thus, shell crushing and shell entry are alternative tactics for feeding on snails (Vermeij 1979, DeWitt et al. 2000, 2003), and a functional trade-off exists between these snail-feeding behaviors. This trade-off may cause diversification in snail-feeding carabid beetles (Sturani 1962, Ishikawa 1978, Sota and Ishikawa 2004, Konuma et al. 2011).

How do beetles with intermediate body shapes (hereafter, intermediate beetles) eat snails? Can intermediate beetles perform both crushing and inserting behaviors, or neither of them? These questions are difficult to assess in the beetle *D. blaptoides*, because intermediate individuals are not observed in the wild (Appendix A). However, we can cross stout and slender subspecies to produce F_1 and backcross hybrids that have intermediately shaped bodies (Konuma et al. 2013). In the present study, we examined the snail-feeding performances of intermediate beetles by comparing the performances of parental individuals and hybrids. We propose a method using logistic regression for estimating trade-off curves with empirical data.

METHODS

We used *Damaster blaptoides capito* (stout-shaped), *D. b. fortunei* (slender-shaped), and their F_1 and two backcross hybrids in feeding experiments (see Appendix B for details about these beetles). Because the details of our crossing design and feeding procedure were described in our previous report (Konuma et al. 2013), we include only an overview here. First, we produced laboratory-reared individuals of *D. b. capito* (hereafter, P_1) and *D. b. fortunei* (P_2) under constant light and temperature conditions (n = 198 and 76, respectively). We reciprocally crossed the males and females of *D. b. capito* and *D. b. fortunei* and produced 107 F_1 hybrids in total. Then we crossed the F_1 hybrids and *D. b. capito* and produced a backcross population to *D. b. capito* (B_1). Similarly, we crossed the F_1 hybrids and *D. b. fortunei* and produced a backcross population to *D. b. fortunei* (B_2). The numbers of B_1 and B_2 individuals were 54 and 79 beetles, respectively. We also confirmed that viability loss due to genetic incompatibility did not exist among these five populations (Appendix B).

We randomly chose 24 individuals (12 males and 12 females) from P_1, P_2, F_1, B_1, and B_2, respectively. Before the feeding experiments, we captured images of the beetles' forebodies (heads and thoraxes) using a digital camera (Camedia C-3040 Zoom, Olympus, Japan) coupled with a microscope (SMZ1500, Nikon, Japan). Using the same focal length as for the beetle images, we captured an image of a 1-mm mesh sheet to use as a scale. By comparing the number of pixels on this scale on the computer screen, we measured the lengths and widths of beetle forebodies from the digital images. Forebody length (L) was defined as the distance from the labrum to the edge of thorax, and forebody width (W) was the width of the thorax. We calculated forebody length divided by forebody width (i.e., L/W) as a forebody slenderness ratio, and used these values as body shape scores to quantify the slenderness (long, narrow) or stoutness (short, wide) of the studied beetles.

Feeding experiments

We examined feeding performances on a small snail species *Discus pauper* and a large snail species *Euhadra quaesita* in this study (see Appendix B for details about these snails). To ensure equivalent feeding motivation among the beetles, we fed them fish sausage (1.5 g) for 12 h to fill their stomachs before each trial. We used this artificial prey instead of land snails because it was difficult to collect a sufficient amount of land snail for 120 beetles at the same time from the wild. During feeding trials with snails, we placed one snail and one beetle in a plastic box (14.0 × 9.0 × 4.5 cm) that contained wet sphagnum moss, and determined whether the beetle succeeded in feeding on the snail within a set time-frame: within 4 h during trials with *D. pauper* and within 96 h for trials with *E. quaesita*. Each beetle was used in only one trial. The difference between these time frames was caused by the size difference between the soft bodies of the snail species; the soft body of *D. pauper* is small and beetles can fully consume it within a few hours, whereas *E. quaesita* is larger and beetles need a few days to consume it fully. It was impossible to determine if beetles that inserted their heads into shells succeeded in feeding on the snails within, because we could not see inside the shell. Therefore, after the trial, we opened the boxes and scored "feeding success" or "feeding failure" based on whether the snail was dead or alive. We used a G test with Williams' correction to detect significant differences in the number of successful feeding trials between *D. b. capito* and F_1 individuals in the test using *D. pauper*, and between *D. b. fortunei* and F_1 individuals in the test using *E. quaesita*.

Trade-off curves

Although many theoretical models of ecological specialization implement trade-offs using simple power functions (Appendix B), we propose the following logistic functions for estimating trade-off curves:

$$f_1 = \frac{1}{1 + e^{-(a_1 x + b_1)}}$$

$$f_2 = \frac{1}{1 + e^{-(a_2 x + b_2)}}$$

where a_1, a_2, b_1, and b_2 are parameters that determine the shape of a trade-off curve. These equations represent trade-off functions if $a_1 a_2 < 0$, that is, if a negative correlation exists between f_1 and f_2. The trade-off is weak (line (1) in Fig. 1A) when f_1 and f_2 are large at intermediate values of x (line (1) in Fig. 1B and C). In contrast, the trade-off is strong (lines (3) and (4) in Fig. 1A) when f_1 and f_2 are small at intermediate values of x (line (3) and (4) in Fig. 1B and C). Although these functions possess more parameters than the power functions that have been used in theoretical models of specialization (Appendix B), the parameter values can be estimated using logistic regression (Janzen and Stern 1998). We estimated those parameters for large snails (f_1) and small snails (f_2), and plotted a trade-off curve by relating f_2 with f_1 based on the body shape parameter, x. Using a straight line that connected the (f_1, f_2) values of the most slender and the stoutest individuals, we determined if the trade-off was strong or weak. To confirm the statistical significance of the strength of a trade-off, we also conducted a test proposed by O'Hara Hines et al. (2004). This method tests the null hypothesis that the fitness of the intermediate phenotype is collinear with those of the divergent phenotypes (line (2) in Fig. 1A) using a chi-square statistics and one-sided P value at $\text{df} = 1$. A significant departure from collinearity with an inward bending curve like line (3) and (4) in Fig. 1A represents a strong trade-off.

RESULTS

Morphology and feeding performances

The body shapes of F_1 and backcross hybrids were intermediate between the parental subspecies (Fig. 2). The slenderness ratio of the F_1 hybrid was larger than that of P_1, *D. b. capito* (ANOVA, $\text{df} = 1, 46$, $F = 62.14$, $P < 0.0001$) but smaller than that of P_2, *D. b. fortunei* (ANOVA, $\text{df} = 1, 46$, $F = 9.82$, $P = 0.003$).

Stouter beetles (with shorter, wider forebodies) succeeded in feeding tests with the small snail *D. pauper* ($P < 0.0001$; Fig. 3A). Because the shell apertures of these snails were much smaller than the beetles' heads, none of the beetles could insert their heads into the shells. However, stouter beetles succeeded in feeding by crushing the shells with their powerful jaws (Fig. 3C). In contrast, more slender beetles (with longer, narrower forebodies) succeeded in feeding tests with the large snail *E. quaesita* ($P = 0.0377$; Fig. 3B). Although the beetles could not crush the shells of these snails, more slender beetles succeeded in feeding by inserting their heads into shells (Fig. 3D). When beetles inserted their heads into shells, the snails retracted their soft tissues deeply within their shells. However, beetles with longer, narrower forebodies succeeded in accessing and feeding on the snails.

Intermediate beetles tried to feed on both small and large snails using both the shell-crushing and shell-entry techniques, but they frequently failed. The feeding success of the F_1 hybrids was lower than that of *D. b.*

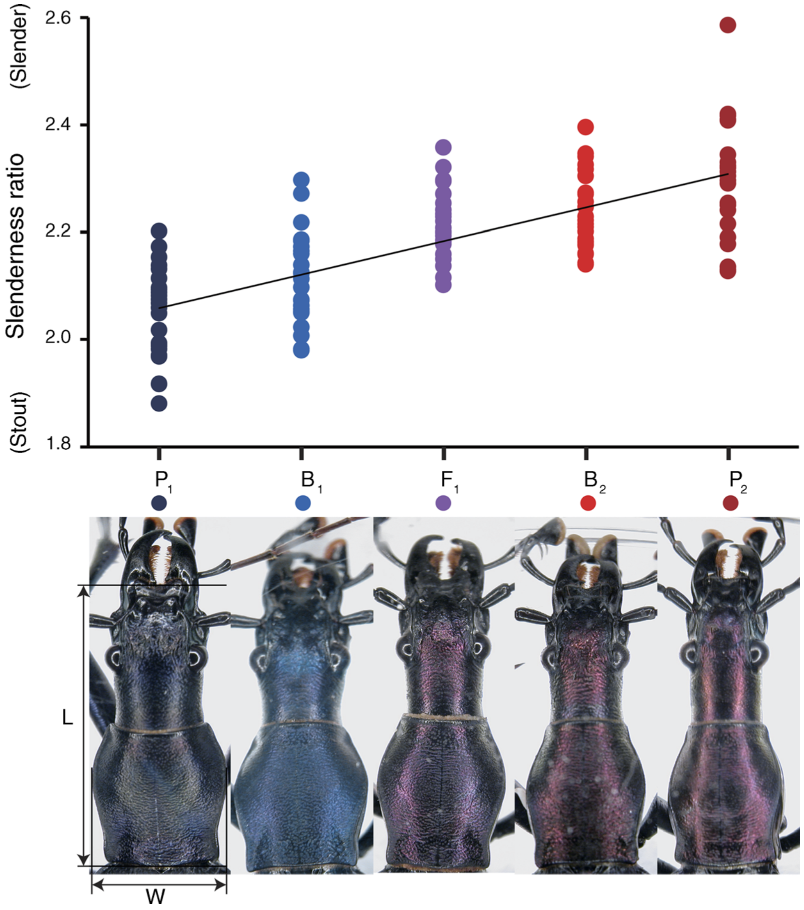

FIG. 2. Slenderness ratios (L/W) of beetle specimens. *Damaster blaptoides capito* (P_1) had a stout forebody, *D. b. fortunei* (P_2) had a slender forebody, and the F_1 and backcross beetles (B_1 and B_2) had an intermediate forebody shape. The black line is a regression line.

capito in tests with small snails (G test, $P = 0.009$), and lower than that of *D. b. fortunei* in tests with large snails (G test, $P = 0.030$).

Trade-off curve

Logistic curves of beetle feeding performances on small and large snails are shown in panels (A) and (B) of Fig. 3, respectively, and the estimated parameters are presented in Appendix C. We drew the (f_1, f_2) curve by connecting these two functions with the parameter x and then plotted the estimated (f_1, f_2) values for all of the experimental individuals (Fig. 4). The resulting plot resembles a strong trade-off curve. The statistical significance of the strong trade-off was confirmed using the method of O'Hara Hines et al. (2004) ($P < 0.05$; Appendix D).

DISCUSSION

Strong trade-off for D. blaptoides

The strong trade-off between the two snail-feeding behaviors suggests that intermediate beetles can be maladapted for snail feeding when beetle fitness is dependent on the availability of large and small snails. Thus, stout and slender beetles are specialists in their particular feeding behaviors, while intermediate beetles are inferior generalists. Disruptive selection that "favors both types of more extreme phenotypes over intermediates" (Rueffler et al. 2006*b*) may have played an important role in the morphological divergence of these beetles.

In the study system with *D. blaptoides*, *D. b. capito* that occurs only on Sado Island possesses a stout body, while all of the other subspecies possess slender bodies (Konuma et al. 2011). Given that *D. b. capito* is phylogenetically close to populations on northern parts of the Japanese mainland (Honshu; Su et al. 1998), the ancestral beetles on Sado Island would have been slender beetles that migrated from Honshu. Thus, a peak shift from a slender to a stout body shape may have occurred after the ancestor of *D. b. capito* colonized Sado Island. This peak shift might have been facilitated by the relative abundance of small-sized land

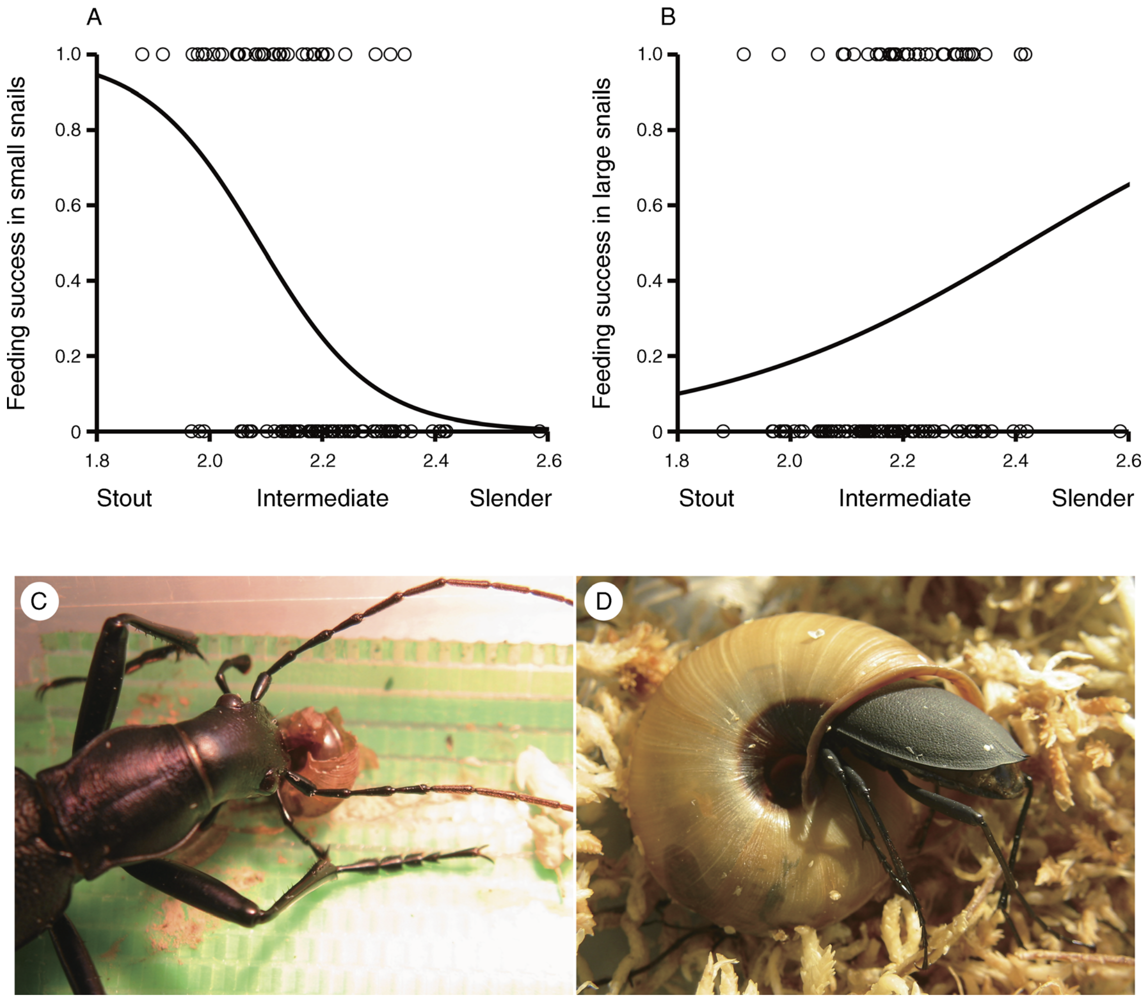

FIG. 3. Snail-feeding performance and body shape differences. (A, C) Stout beetles had higher success rates for feeding on small snails (*Discus pauper*) because they could crush snail shells. (B, D). Slender beetles had higher success rates for feeding on larger snails (*Euhadra quaesita*) because they could insert their heads into the shells. Circles indicate feeding success or feeding failure (1.0 represents that beetles succeeded in feeding on land snails; 0 represents that beetles failed in feeding on snails) and curves are logistic regressions.

snails on Sado Island, as was suggested by our previous analysis that found a negative correlation between the average size of representative land snails in the genus *Euhadra* and the stoutness of the *D. blaptoides* body shape (Konuma et al. 2011). However, we have insufficient information to determine if small snails have been dominant on Sado Island (Appendix B). Detailed investigations of snail fauna will be important for understanding divergence in *D. blaptoides*.

Ecological specialization in animal trophic morphology

Forister et al. (2012) reviewed the concept of the evolution of ecological specialization for insect–plant interactions, and suggested that evidence for trade-offs has remained insufficient to generally explain specialization. Given that positive, but not negative, correlations are observed in most experiments of cross-host correlations with juvenile performances (Fry 1996), an explanation based on the trade-off principle may be invalid for the evolution of ecological specialization in phytophagous insects. In fact, the same patterns of specialization can be theoretically explained without assuming that trade-offs exist (Whitlock 1996). Theoretical conditions under which weak trade-offs select for specialists and strong trade-offs select for generalists can also be found in Rueffler et al. (2006*a*, 2013).

However, the present study suggests that a functional trade-off in snail-feeding performances exists and may result in selection against intermediate beetles. Other recent studies have also suggested that functional trade-offs may exist in the trophic morphologies and behaviors of animals such as finches (Herrel et al.

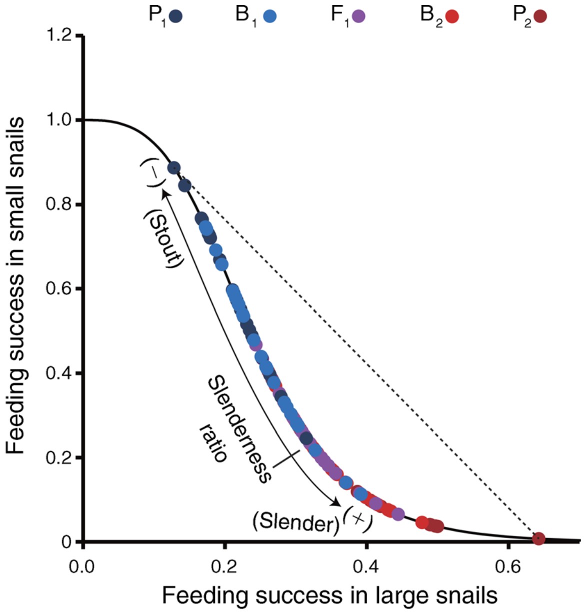

FIG. 4. Trade-off curve for snail-feeding performances. Colored circles indicate the estimated feeding performances according to the slenderness ratio (see Fig. 2). A dotted line connects the feeding performance values of the most slender and stoutest individuals.

2009), bats (Santana and Dumont 2009), and skinks (Vanhooydonck et al. 2011). These studies suggest that trade-offs result in the evolution of ecological specialization and character diversification.

Compared with morphological and behavioral analyses of animal trophic traits, it may be relatively difficult to detect negative correlations in the performances of phytophagous larvae among different hosts, because subtle phenotypic differences may result in differences in the performances of the hosts (Scheirs et al. 2000, Forister et al. 2012). The paucity of publications that support trade-offs may be due to a failure to detect evidence, even though many studies have sought to demonstrate trade-offs (Futuyma 2008). As suggested by Forister et al. (2012), genomic approaches would be effective for verifying the effect of the genetic architecture on the evolution of ecological specialization in phytophagous insects. By examining historical processes of loss-of-function in genes, one can verify how adaptive decay and ecological specialization occur (Ostrowski et al. 2007) without evidence of trade-offs. Genomics and transcriptomics approaches should be used to examine how animal trophic morphologies specialize in niches and diversify, given genetic and developmental constraints (Brakefield 2006, Losos 2011, Persons et al. 2011). Genetic and developmental studies are important next steps for understanding diversification in the snail-feeding carabid beetles.

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LITERATURE CITED

Benkman, C. W. 1993. Adaptation to single resources and the evolution of Crossbill (*Loxia*) diversity. Ecological Monographs 63:305–325.

Brakefield, P. M. 2006. Evo-devo and constraints on selection. Trends in Ecology and Evolution 21:362–368.

DeWitt, T. J., and R. B. Langerhans. 2003. Multiple prey traits, multiple predators: keys to understanding complex community dynamics. Journal of Sea Research 49:143–155.

DeWitt, T. J., B. W. Robinson, and D. S. Wilson. 2000. Functional diversity among predators of a freshwater snail imposes an adaptive trade-off for shell morphology. Evolutionary Ecology Research 2:129–148.

Forister, M. L., L. A. Dyer, M. S. Singer, J. O. Stireman III, and J. T. Lill. 2012. Revisiting the evolution of ecological specialization, with emphasis on insect–plant interactions. Ecology 93:981–991.

Fry, J. D. 1996. The evolution of host specialization: are trade-offs overrated? American Naturalist 148:S84–S107.

Futuyma, D. J. 2008. Sympatric speciation: norm or exception? Pages 136–148 *in* K. J. Tilmon, editor. Specialization, speciation and radiation: the evolutionary biology of herbivorous insects. University of California Press, Berkeley, California, USA.

Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. Annual Review of Ecology, Evolution, and Systematics 19:207–233.

Gavrilets, S., and J. B. Losos 2009. Adaptive radiation: contrasting theory with data. Science 323:732–737.

Hatfield, T., and D. Schluter. 1999. Ecological speciation in sticklebacks: environment-dependent hybrid fitness. Evolution 53:866–873.

Herrel, A., J. Podos, B. Vanhooydonck, and A. P. Hendry. 2009. Force–velocity trade-off in Darwin's finch jaw function: a biomechanical basis for ecological speciation? Functional Ecology 23:119–125.

Ishikawa, R. 1978. A revision of the higher taxa of the subtribe Carabina (Coleoptera, Carabidae). Bulletin of the National Science Museum, Series A (Zoology) 5:95–114.

Janzen, F. J., and H. S. Stern. 1998. Logistic regression for empirical studies of multivariate selection. Evolution 52: 1564–1571.

Konuma, J., and S. Chiba. 2007. Trade-offs between force and fit: extreme morphologies associated with feeding behavior in carabid beetles. American Naturalist 170:90–100.

Konuma, J., N. Nagata, and T. Sota. 2011. Factors determining the direction of ecological specialization in snail-feeding carabid beetles. Evolution 65:408–418.

Konuma, J., T. Sota, and S. Chiba. 2013. Quantitative genetic analysis of subspecific differences in body shape in the snail-feeding carabid beetle *Damaster blaptoides*. Heredity 110:86–93.

Levins. R. 1962. Theory of fitness in a heterogeneous environment. I. The fitness set and the adaptive function. American Naturalist 96:361–373.

Losos, J. B. 2011. Seeing the forest for the trees: the limitations of phylogenies in comparative biology. American Naturalist 177:709–727.

O'Hara Hines, R. J., W. G. S. Hines, and B. W. Robinson. 2004. A new statistical test of fitness set data from reciprocal transplant experiments involving intermediate phenotypes. American Naturalist 163:97–104.

Ostrowski, E. A., C. Ofria, and R. E. Lenski. 2007. Ecological specialization and adaptive decay in digital organisms. American Naturalist 169:E1–E20.

Parsons, K. J., and B. W. Robinson. 2007. Foraging performance of diet-induced morphotypes in pumpkinseed sunfish (*Lepomis gibbosus*) favours resource polymorphism. Journal of Evolutionary Biology 20:673–684.

Ravigné, V., U. Dieckmann, and I. Olivieri. 2009. Live where you thrive: joint evolution of habitat choice and local adaptation facilitates specialization and promotes diversity. American Naturalist 174:E141–E169.

Rueffler, C., M. Egas, and J. A. J. Metz. 2006*a*. Evolutionary predictions should be based on individual-level traits. American Naturalist 168:148–162.

Rueffler, C., J. A. J. Metz, and T. J. M. Van Dooren. 2013. What life cycle graphs can tell about the evolution of life histories. Journal of Mathematical Biology 66:225–279.

Rueffler, C., T. J. M. Van Dooren, O. Leimar, and P. A. Abrams. 2006*b*. Disruptive selection and then what? Trends in Ecology and Evolution 21:238–245.

Rueffler, C., T. J. M. Van Dooren, and J. A. J. Metz. 2004. Adaptive walks on changing landscapes: Levins' approach extended. Theoretical Population Biology 65:165–178.

Rueffler, C., T. J. M. Van Dooren, and J. A. J. Metz. 2006*c*. The evolution of resource specialization through frequency-dependent and frequency-independent mechanisms. American Naturalist 167:81–93.

Santana, S. E., and E. R. Dumont. 2009. Connecting behaviour and performance: the evolution of biting behaviour and bite performance in bats. Journal of Evolutionary Biology 22: 2131–2145.

Scheirs, J., L. De Bruyn, and R. Verhagen. 2000. Optimization of adult performance determines host choice in a grass miner. Proceedings of the Royal Society B 267:2065–2069.

Schluter, D. 1993. Radiation in sticklebacks: size, shape, and habitat use efficiency. Ecology 74:699–709.

Schluter, D. 2000. The ecology of adaptive radiation. Oxford University Press, Oxford, UK.

Sota, T., and R. Ishikawa. 2004. Phylogeny and life-history evolution in *Carabus* (subtribe Carabina: Coleoptera, Carabidae) based on sequences of two nuclear genes. Biological Journal of the Linnean Society 81:135–149.

Sturani, M. 1962. Osservazioni e ricerche biologishce sul genere Carabus Linnaeus (sensu lato). Estratto dalle Memorie della Societa Entomologica Italiana 41:85–202.

Su, Z., O. Tominaga, M. Okamoto, and S. Osawa. 1998. Origin and diversification of hindwingless *Damaster* ground beetles within the Japanese islands as deduced from mitochondrial ND5 gene sequences (Coleoptera, Carabidae). Molecular Biology and Evolution 15:1026–1039.

Vanhooydonck, B., R. Boistel, V. Fernandez, and A. Herrel. 2011. Push and bite: trade-offs between burrowing and biting in a burrowing skink (*Acontias percivali*). Biological Journal of the Linnean Society 102:91–99.

Vermeij, G. J. 1979. Shell architecture and causes of death of Micronesian reef snails. Evolution 33:686–696.

Whitlock, M. C. 1996. The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. American Naturalist 148:S65–S77.

Wilson, D. S., and J. Yoshimura. 1994. On the coexistence of specialists and generalists. American Naturalist 144:692–707.

Supplemental Material

Appendix A

Geographic distribution and morphology in *Damaster blaptoides* (*Ecological Archives* E094-241-A1).

Appendix B

Detailed description of the carabid beetles, land snails, and trade-offs in previous studies (*Ecological Archives* E094-241-A2).

Appendix C

The result of the logistic regressions (*Ecological Archives* E094-241-A3).

Appendix D

Statistical significance of the trade-off (*Ecological Archives* E094-241-A4).