

Imbalance of Predator and Prey Armament: Geographic Clines in Phenotypic Interface and Natural Selection

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ABSTRACT: The escalation of defensive/offensive arms is ubiquitous in prey-predator evolutionary interactions. However, there may be a geographically varying imbalance in the armaments of participating species that affects the outcome of local interactions. In a system involving the Japanese camellia (*Camellia japonica*) and its obligate seed predator, the camellia weevil (*Curculio camelliae*), we investigated the geographic variation in physical defensive/offensive traits and that in natural selection on the plant's defense among 17 populations over a 700-km-wide area in Japan. The sizes of the plant defensive apparatus (pericarp thickness) and the weevil offensive apparatus (rostrum length) clearly correlated with each other across populations. Nevertheless, the balance in armaments between the two species was geographically structured. In the populations for which the balance was relatively advantageous for the plant's defense, natural selection on the trait was stronger because in the other populations, most plant individuals were too vulnerable to resist the attacks of the weevil, and their seeds were infested independent of pericarp thickness. We also found that the imbalance between the defensive/offensive armaments and the intensity of natural selection showed clear latitudinal clines. Overall, our results suggest that the imbalance of armament between sympatric prey and predator could determine the strength of local selection and that climatic conditions could affect the local and overall trajectory of coevolutionary arms races.

Keywords: coevolution, arms race, geographic mosaic, predator-prey interactions, latitudinal gradient, exaggeration.

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Interspecific interactions are one of the most important driving forces of organismal evolution (Darwin 1859; Ehrlich and Raven 1964; van Valen 1973; Thompson 1994; Vermeij 1994). In the wild, most organisms must defend themselves against predators or parasites, and the exploiters have to cope with the strengthened defenses of their prey. Hence, the exaggeration of defensive and offensive characters is expected (Dawkins and Krebs 1979; Abrams 1986; Saloniemi 1993; Sasaki and Godfray 1999; Abrams 2000). In fact, elaborated armaments are ubiquitous in nature (Vermeij 1987; West et al. 1991; Benkman 1999; Brodie and Brodie 1999; Benkman et al. 2001; Dietl 2003).

To clarify the dynamics of interspecific interactions, investigating only one or two populations is insufficient for characterizing all the properties of the focal system. In the geographic mosaic theory of coevolution, Thompson (1994, 1999a, 1999b, 2005) has argued that the natural selection imposed by interacting participants varies among populations ("selection mosaic"; Benkman 1999; Benkman et al. 2001; Rudgers and Strauss 2004). As a result, reciprocal selection occurs in some localities ("coevolutionary hotspots") and not in others ("coevolutionary coldspots"). Moreover, gene flow may remix the coevolving characters between those hotspots and coldspots (Hochberg and van Baalen 1998; Nuismer et al. 1999; Gomulkiewicz et al. 2000; Nuismer et al. 2000; Brockhurst et al. 2003; Forde et al. 2004), thereby causing local maladaptation in some localities (Thompson et al. 2002). Consequently, species-to-species interactions occur at the population level, and it is only when the nature of interactions at the population level is revealed that we can fully reconstruct or predict the overall evolutionary dynamics of focal interactions (Thompson 1994, 1999a, 1999b, 2005).

The geographic view of species interactions leads to predictions that characters shaped by interactions will vary among populations (Dybdahl and Lively 1996; Benkman 1999; Kraaijeveld and Godfray 1999; Lively and Dybdahl 2000; Benkman et al. 2001; Brodie et al. 2002; Geffney et al. 2002, 2005; Thompson and Cunningham 2002; San-

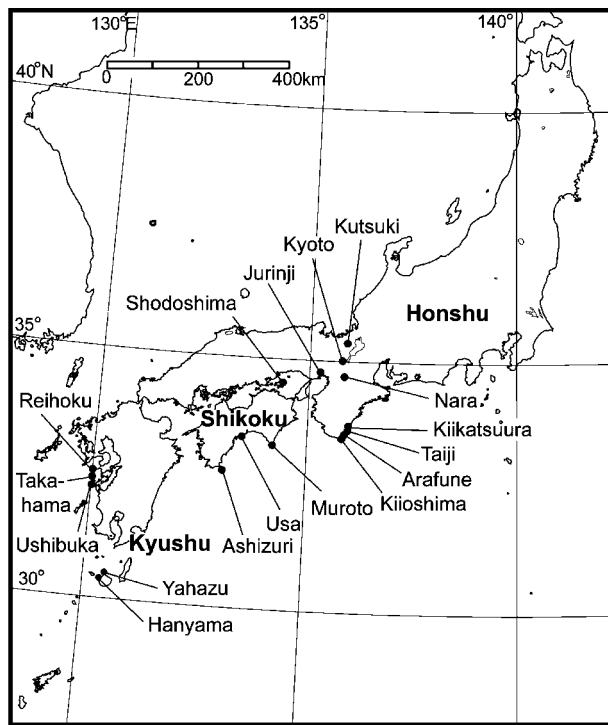


Figure 1: Map of the 17 study sites.

ford et al. 2003; Thrall and Burdon 2003; Zangerl and Berenbaum 2003) and that the traits of interacting species will match in some localities but mismatch in others (Dybdahl and Lively 1996; Benkman 1999; Benkman et al. 2001; Brodie et al. 2002; Zangerl and Berenbaum 2003). For example, in the system involving the rough-skinned newt *Taricha granulose* and the garter snake *Thamnophis sirtais*, which eats the newt, the tetrodotoxin (TTX) toxicity of the newt and the resistance of the snake to the toxin vary geographically, and the two traits are correlated with each other across populations (Hanifin et al. 1999; Brodie et al. 2002). This fact is congruent with the hypothesis that coevolutionary arms races occurred between toxicity and resistance in some populations (hotspots) but that in other

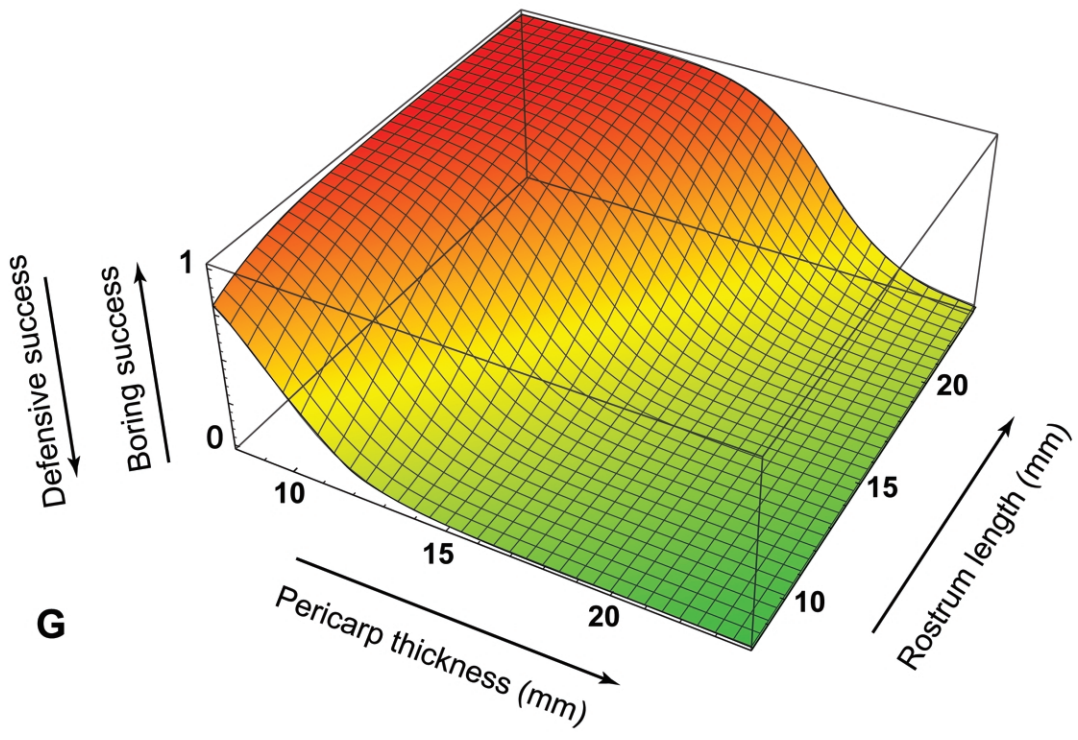
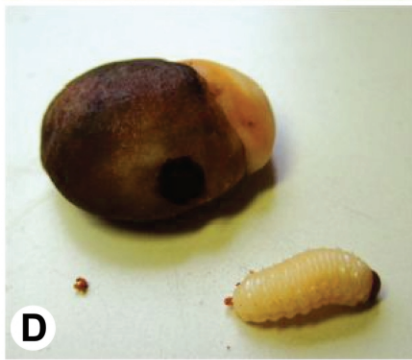
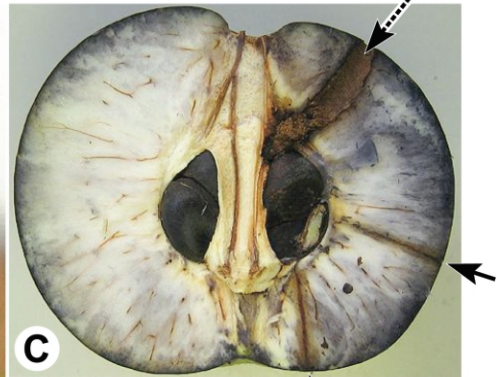
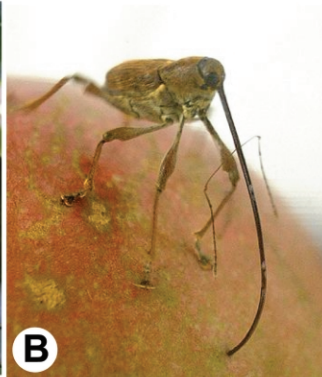
populations (coldspots), little or no reciprocal evolution has occurred (Brodie et al. 2002).

Although such correlation or matching between prey/predator phenotypes provides crucial insights into geographically structured processes of species interactions, a further look at the phenotypic interface of interactions raises another question. Even if the phenotypes of interacting species are correlated with each other across populations, the imbalance in armaments between those traits can be heterogeneous, and the phenotypic association may be more advantageous for one species in some populations compared with other populations (Brodie and Brodie 1999). For example, garter snakes in a coevolutionary hotspot would be highly resistant to TTX, but they might be critically damaged by eating a highly toxic sympatric newt. Conversely, snakes in a coldspot would have low resistance to TTX, but they might not suffer if sympatric newts were almost nonpoisonous (Brodie and Brodie 1991, 1999).

If the imbalance of armament between prey and predator varied among populations, the evolutionary processes of interactions would also be structured geographically. In particular, the direction and intensity of natural selection on respective defensive and offensive traits could be heterogeneous over geographic landscapes given that the nature of selection on those traits is determined by the combination of the phenotypic distribution of the focal species and that of participating species (Brodie and Brodie 1999; Brodie and Ridenhour 2003; Ridenhour 2005). Although this problem of local phenotypic interface is crucial for understanding the geographic mosaic of species interactions, few studies have evaluated the local balance in armaments between interacting species over a broad geographic area.

To reveal the local imbalance of defensive/offensive armaments between prey and predator and to examine its potential effects on the geographic structure of the outcome of interactions, we investigated a system involving an evergreen broad-leaved tree, *Camellia japonica* (Japanese camellia; Theaceae), and its obligate seed predator, *Curculio camelliae* (camellia weevil; Coleoptera: Curculionidae; figs. 1, 2A–2F) across 17 populations spanning

Figure 2: Interacting species: Japanese camellia and the camellia weevil. *A*, A flower of Japanese camellia. *B*, A female camellia weevil drilling with her long rostrum into the pericarp of a Japanese camellia fruit (see videos 1 and 2 in the online edition of the *American Naturalist*). *C*, A cross-section of a fruit showing narrow holes in the woody pericarp that were made by female weevils (solid arrow) and an exit hole of a weevil larva (dashed arrow). *D*, A larva of the weevil with an infested seed. *E*, The geographic variation in the fruit size of Japanese camellia. The ordinary-sized fruit was collected in Kyoto (left), and the maximum-sized fruit was obtained in Hanyama (right). *F*, The geographic variation in the rostrum length of the camellia weevil. A female from Kyoto (below) and one from Hanyama (above). *G*, The phenotypic interface between the plant's defense and the weevil's offense inferred from an experiment. The probability of successful boring of a Japanese camellia pericarp by a female camellia weevil was regressed on the pericarp thickness of the plant and the rostrum length of the weevil. The surface is fitted using a generalized linear mixed model in which binomial error and logit-link function were applied.



700 km in Japan (fig. 1). The larva of the weevil feeds exclusively on the seeds of Japanese camellia, and the adult female excavates the thick pericarp of the plant with its extremely long rostrum for oviposition (Saito and Suzuki 1982; Okamoto 1988a, 1988b; fig. 2A–2F; see also videos 1 and 2 in the online edition of the *American Naturalist*). Our approach here was threefold. First, in an experiment, we evaluated the impact of the pericarp thickness of the plant and the rostrum length of the weevil on the fitness of each participant. Second, based on the results of the experiment, the imbalance of armaments between the two species was evaluated for each population. Finally, ecological properties, such as severity of seed infestation, were compared among the populations, and the geographic variation in natural selection on the plant's defense in each locality was quantified.

Material and Methods

Study Organisms

Japanese camellia (*Camellia japonica* L.) is a popular ornamental species that bears large cardinal flowers (fig. 2A). The plant is highly self-incompatible and is pollinated by birds (Kunitake et al. 2004). In the wild, it occurs in the warm temperate forests of Japan and the southern Korean Peninsula (Wendel and Parks 1985; Chung and Kang 1996; Oh et al. 1996; Chung and Chung 2000; Ueno et al. 2002; Chung et al. 2003). This woody plant grows up to 15 m in height, and its generation time is decades.

This species is conspicuous for its large fruit: one of the native varieties that bears especially large fruit (maximum diameter 8.5 cm) is called "apple camellia" (*C. japonica* var. *macrocarpa*; fig. 2E). Each fruit usually contains up to 10 seeds surrounded by woody, very thick pericarp, which dehisces after seed maturation. The thickness of the pericarp is extraordinary in the genus *Camellia* and its sister taxa in the tribe Theeae (Sealy 1958; Keng 1962; Satake et al. 1989; see Prince and Parks 2001 for the phylogeny of Theaceae).

To reveal the factors that govern the exaggerated pericarp of Japanese camellia, Okamoto (1988a, 1988b) focused on an obligate seed predator, *Curculio camelliae* Roelofs (camellia weevil; Coleoptera: Curculionidae; fig. 2B), and suggested that natural selection imposed by this insect has driven the evolution of a thick pericarp. The female of this seed-predatory weevil bores a hole through the pericarp of Japanese camellia with its extremely long rostrum (fig. 2B, 2C), and, after reaching a seed, it pulls out the rostrum and then inserts its long ovipositor to deposit an egg in the seed (Okamoto 1988a, 1988b). Seed infestation by weevil larvae often affects more than half of the seed crop (Saito and Suzuki 1982; Okamoto 1988a, 1988b),

and this weevil has the greatest effect on the seed mortality of the plant. Okamoto (1988a, 1988b) found that fruit with a thicker pericarp could circumvent penetration by the rostrum of the weevil and thereby avoid damage to its seeds.

Weevils in the genus *Curculio* infest the seeds of Fagaceae, Juglandaceae, Theaceae, Betulaceae, and others (Menu 1993; Maeto and Ozaki 2003; Hughes and Vogler 2004a, 2004b). *Curculio camelliae* is an agricultural pest of Japanese camellia seeds, which are the raw material of camellia oil. The adults emerge in April to May (Saito and Suzuki 1982; H. Toju, personal observation), and they copulate on the fruit of Japanese camellia from June to August (H. Toju, personal observation). Oviposition occurs after the pericarp of the Japanese camellia almost finishes its growth (June to August; Saito and Suzuki 1982; H. Toju, personal observation); fruit that has yet to reach the maximum size contains small, undeveloped seeds filled with jelly-like endosperm, which appears unsuitable for oviposition (Okamoto 1988a). A larva usually consumes one seed and develops to the fourth instar within 1 month (fig. 2D); it then leaves the fruit and overwinters in the soil (Saito and Suzuki 1982). The duration of dormancy is not clear, although Saito and Suzuki (1982) and Okamoto (1988a) have reported that larvae did not emerge as adults after passing one winter in the laboratory. During the dormant period, the larva is potentially infected by fungal parasites, such as species of *Beauveria* and *Metarrhizium* (Saito and Suzuki 1982). The distribution of this obligate seed predator (Kojima and Morimoto 2004) largely matches that of the Japanese camellia, but in some islands off mainland Japan, the weevil is absent (e.g., the Izu Islands; Saito and Suzuki 1982).

Sampling Strategy

We conducted a field study over almost the entire range of Japanese camellia and camellia weevil in Japan (fig. 1; table 1). In August and September 2003, Japanese camellia fruits were collected from each site about 1 month after the oviposition season of the camellia weevil. To avoid overexploitation, we collected less than one-third of the fruit from individual trees; up to eight fruits were sampled for each tree at random. For each locality, we chose trees randomly, although most trees were sampled when the population size was small. As fruit size is affected by the degree of maturation, only fruits containing seeds filled with cotyledons were selected for subsequent analyses (in total, 965 fruits from 530 trees in 17 localities). In addition, we sampled female camellia weevils at each site from 2002 to 2004 (272 individuals from 15 localities).

Table 1: Study sites and the morphology of the camellia weevil (*Curculio camelliae*) and the Japanese camellia (*Camellia japonica*)

Locality	Latitude (°N)	Longitude (°E)	N	<i>Curculio camelliae</i>			<i>Camellia japonica</i>					
				Body length ^a (mm)	Rostrum length ^a (mm)	No. trees	No. fruits	No. seeds	Fruit diameter ^a (mm)	Pericarp thickness ^a (mm)	CV (%)	Seed/ fruit
Kutsuki	35.367	135.913	7	8.19 ± .18	10.42 ± .61	25	44	178	30.04 ± 3.05	6.07 ± .87	14.3	3.5
Kyoto	35.017	135.813	19	7.86 ± .55	9.89 ± 1.02	21	23	73	30.18 ± 3.57	6.30 ± 1.65	26.1	3.2
Jurinji	34.775	130.313	23	7.83 ± .35	10.31 ± .93	32	61	238	30.88 ± 3.04	6.13 ± 1.20	19.5	4.1
Shodoshima	34.508	134.363	28	44	259	39.51 ± 5.69	8.03 ± 1.81	22.5	5.8
Nara	34.692	135.875	4	7.53 ± .45	10.05 ± .87	37	86	480	36.76 ± 3.55	6.66 ± 1.38	20.7	5.5
Kiikatsuura	33.650	135.988	9	7.75 ± .56	10.66 ± 1.17	27	34	212	39.14 ± 7.58	7.73 ± 2.47	31.9	6.1
Taiji	33.583	135.963	10	7.35 ± .51	9.12 ± .74	17	37	248	40.44 ± 3.54	6.76 ± 1.14	16.8	6.7
Arafune	33.533	135.888	8	7.42 ± .26	9.21 ± .69	37	58	319	38.49 ± 3.73	6.42 ± 1.08	16.8	5.6
Kiioshima	33.467	135.863	22	7.73 ± .37	9.61 ± .59	19	46	173	35.27 ± 5.66	7.52 ± 1.47	19.6	3.3
Muroto	33.250	134.188	20	7.50 ± .32	10.06 ± .66	37	55	310	37.35 ± 4.26	7.77 ± 1.69	21.8	5.5
Usa	33.425	133.463	5	8.21 ± .38	13.63 ± .91	33	50	316	44.54 ± 6.24	11.65 ± 2.82	24.2	6.4
Ashizuri	32.725	133.025	10	8.05 ± .43	12.98 ± .93	67	102	521	49.10 ± 6.58	12.80 ± 2.45	19.2	4.9
Reihoku	32.525	130.025	46	7.87 ± .42	11.68 ± .94	39	62	350	45.87 ± 7.05	11.89 ± 2.61	21.9	5.6
Takahama	32.342	129.975	56	7.77 ± .34	11.48 ± .70	39	93	619	47.96 ± 6.71	11.13 ± 2.68	24.1	6.5
Ushibuka	32.158	130.025	10	18	122	46.40 ± 5.09	9.94 ± 2.41	24.2	6.7
Yahazu	30.458	130.500	20	8.30 ± .50	14.54 ± 1.87	41	101	512	48.09 ± 8.08	12.49 ± 3.39	27.2	4.8
Hanyama	30.383	130.388	13	9.31 ± .68	19.48 ± 1.85	21	51	365	64.87 ± 7.78	20.41 ± 3.99	19.5	6.9

Note: Sample sizes, the coefficient of variation calculated for the pericarp thickness of the Japanese camellia, and the average number of seeds per fruit are also shown.

^a Mean ± SD.

Measurement of Morphology

The fruit morphology of Japanese camellia was measured to the nearest 0.01 mm using digital calipers. The fruit diameter was measured as the mean of a longitudinal diameter and two equatorial diameters that were perpendicular to each other. The pericarp thickness was the mean of four measurements along cross-axes of a longitudinal section of the fruit. The two measurements were averaged over individual trees. The rostrum length and body length (head margin excluding the rostrum to the elytral apex) of the camellia weevil were measured on images taken with a digital camera (IXY Digital 400; Canon) using the software Image J (Sun Microsystems). The mean values of the characters were then calculated for each population, and the correlation between pericarp thickness and rostrum length was examined. In addition, each of the two characters was regressed on the latitude (°N) of each sampling locality (linear regression). ANCOVA was performed to test whether the latitudinal gradients of predator and prey characters differ from each other. The two traits were \log_{10} -transformed before the statistical analysis.

Phenotypic Interface of Prey/Predator Traits: An Experiment

We used fruit and weevils collected on Yakushima Island in Kagoshima Prefecture to determine the probability of

successful penetration of the pericarp (boring success) for a given rostrum length of camellia weevil and pericarp thickness of Japanese camellia. We presented one intact fruit (pericarp thickness 7.89–25.06 mm) to one female camellia weevil in a cylindrical plastic case (diameter 115 mm, height 98 mm) and let the weevil bore the fruit for 24 h (197 fruit-weevil pairs). The females (34 individuals, rostrum length 8.58–20.12 mm) were used repeatedly for four to nine trials. For each hole made by the weevil, we judged whether it reached the inner surface of the pericarp (a total of 553 of 977 holes reached the seeds). As fruits with no trial holes were not informative in this analysis, the sample size consequently became 30 weevils and 105 fruit-weevil pairs. To infer the interaction fitness function (Brodie and Ridenhour 2003) for boring success, we built a generalized linear mixed model (penalized quasi-likelihood procedure) with binomial error and a logit-link function using the statistical package R, version 2.10 (<http://www.r-project.org/>). A logistic function is suitable for binomial data, in this case, the success/failure of excavation of the pericarp by the weevil (Janzen and Stern 1998). Pericarp thickness and rostrum length were used as fixed terms, and the individual weevil used in the experimental trials and each fruit nested within them were fitted as random terms to control for repeated measures within weevil individuals and Japanese camellia fruit. The function was visualized in a three-dimensional graph (range of defensive/offensive characters 8–24 mm).

The interaction fitness function provides insight into the underlying mechanistic relationship between the prey and predator. Based on the function, one can infer the direction and intensity of selection for a focal population if the phenotypic distributions of both interacting species are provided (Brodie and Ridenhour 2003). In this sense, we calculated the condition in which the probability of successful boring equals 50%. In the case of a bivariate logistic regression, it emerges when $a + b_1x_1 + b_2x_2 = 0$, where x_1 and x_2 denote predictor variables (for the interaction fitness function, the phenotypes of respective interacting species). This formula represents a line we call the P_{BS50} line, and around this area of phenotypic distribution, selection on respective prey/predator traits is theoretically most intense because the slope of the fitness function become steepest at inflexion points on both axes of the predictor variables. The standard error of the P_{BS50} line was obtained using the delta method (Bishop et al. 1975).

Geographic Variation in Natural Selection

To characterize the interaction between the Japanese camellia and the camellia weevil for each locality, we used two estimates. First, the ratio of holes reaching seeds to the total holes bored by female camellia weevils (the proportion of successful excavation p_{SE}) was calculated (8,251 of 17,702 holes reached seeds; two sites, Shodoshima and Ushibuka, were excluded owing to the small sample size of trial holes). Holes less than 2 mm deep were ignored because they were indistinguishable from scratches produced by other biotic/abiotic factors. Second, the numbers of infested/uninfested seeds were counted in each population, and the proportion of infested seeds (p_{IS}) was obtained (1,242 of 5,295 seeds were infested). The two estimates were regressed on latitude (linear regression); and the assumptions of normality and homoscedasticity were confirmed.

Before quantifying the strength of natural selection on the pericarp thickness of the plant, the coefficient of variation (CV) among individual trees was calculated for each site in order to detect the presence of phenotypic variation. In addition, a nested ANOVA, in which individual trees were nested within localities, was performed to confirm the presence of interindividual variation (trees with only one sample fruit were excluded from this statistic).

Natural selection on the pericarp thickness of Japanese camellia was evaluated for each population. For each tree, surviving/infested mature seeds were counted, and the percentage of surviving seeds was used as a fitness measure. Note that ovules or seeds that died before maturation (presumably owing to a failure of fertilization, abortion, or infestation by female camellia weevils themselves) were

excluded from this analysis because they were sometimes so small that we could not fully identify them. In addition, the loss of fitness would differ depending on whether the infested seeds were mature or were immature ones that had not been allocated resources; consequently, they should not be treated equally. Accordingly, our analyses concentrated on one selection episode: seed infestation by the weevil larvae; no other mortality factor affecting mature seeds was observed from our sampling. Linear and quadratic selection coefficients were analyzed to detect directional or stabilizing/disruptive selection (Lande and Arnold 1983; Arnold and Wade 1984; Brodie et al. 1995). In the regressions, the fitness of individual trees was divided by the mean fitness of the focal population (relative fitness). To clarify the pattern of the geographic variation in natural selection on pericarp thickness, standardized linear selection coefficients (Lande and Arnold 1983; Arnold and Wade 1984; Hereford et al. 2004) were regressed on latitude.

Results

The Interaction Fitness Function

The experiment in which one Japanese camellia fruit was provided to one female camellia weevil revealed a clear relationship between the probability of boring success and the defensive/offensive characters (fig. 2G). The interaction fitness function constructed using a multiple logistic regression was

$$P_{BS} = \frac{1}{1 + \exp(0.819x - 0.470y - 4.18)},$$

where P_{BS} , x , and y denote the probability of boring success, pericarp thickness, and rostrum length, respectively (coefficients for x : SE = 0.079, df = 74, $t = -10.4$, $P < .0001$; y : SE = 0.098, df = 28, $t = 4.81$, $P < .0001$; intercept: SE = 1.60, df = 872, $t = 2.61$, $P < .01$). Figure 2G clearly shows that the longer the weevil rostrum, the greater the probability of successful boring, whereas a thicker pericarp of Japanese camellia more successfully prevented penetration. From the equation, we anticipated that half of the trials of the camellia weevil would be successful when $y = 1.74x - 8.90$ (fig. 3A; see below); the standard error of the P_{BS50} line was

$$y = \pm \sqrt{0.123x^2 - 3.46x + 24.5}.$$

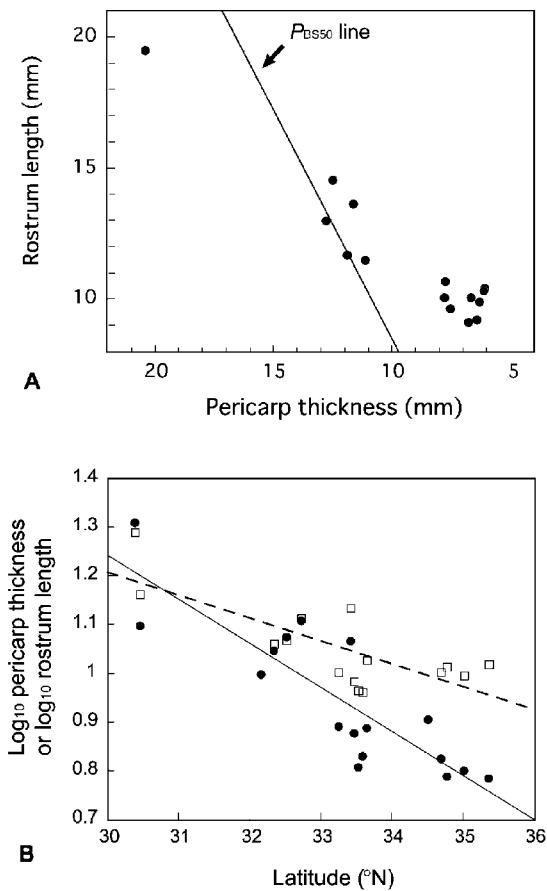


Figure 3: Geographic variation in defensive/offensive traits. *A*, The two-dimensional surface of mean pericarp thickness and mean rostrum length. The P_{BSS0} line, on which half of the trial bores of the camellia weevil are estimated to reach seeds, was plotted (arrow; see text). Note that the axis of pericarp thickness is arranged from high to low in order to clarify the geographic pattern appearing in *B* and figure 4A, 4C (geographic clines along latitude). Accordingly, plots on the right side represent northern populations, and those on the left are southern populations. *B*, The clinal variation in the mean pericarp thickness of the Japanese camellia (circle; solid line) and mean rostrum length of the camellia weevil (square; dashed line) along latitude.

Geographic Variation in Prey/Predator Traits

In the geographic sampling over a 700-km-wide range in Japan, remarkable interpopulation variation was observed for both the pericarp thickness of the Japanese camellia (6.07–20.41 mm) and the rostrum length of the camellia weevil (9.12–19.48 mm; table 1; fig. 3A). In addition, for the plant, the increase in the pericarp thickness was disproportional compared with the rest of the fruit tissues, including seeds (table 1). The geographic differentiation in these phenotypes was observed on a very small spatial scale. For example, the mean pericarp thickness of Japanese camellia was about 8 mm thicker in Hanyama than

in Yahazu (Welch's test; $df = 1$, $F = 60.4$, $P < .0001$) even though only 14 km separated these two populations. Consistently, the mean rostrum length was also about 5 mm longer in the former locality than in the latter (Welch's test; $df = 1$, $F = 55.7$, $P < .0001$).

There was a clear correlation between the means of pericarp thickness and rostrum length across populations (Pearson's correlation; $N = 15$, $r = 0.95$, $P < .0001$; fig. 3A). In addition, on the two-dimensional surface of the defensive and offensive characters, the distance from the P_{BSS0} line, on which half of the trial holes made by the weevil will reach seeds of Japanese camellia, varied among populations (fig. 3A). Therefore, the balance in armaments is relatively advantageous for the weevil side in the populations on the right of the line, whereas, in the populations plotted on the left of the line, the Japanese camellia should more likely be able to defend its seeds against the weevil. Moreover, we found that both characters were greater in more southern localities (\log_{10} pericarp thickness = $3.95 - 0.0901 \times \text{latitude}$, $N = 17$, $F = 43.4$, $P < .0001$; \log_{10} rostrum length = $2.61 - 0.0469 \times \text{latitude}$, $N = 15$, $F = 18.8$, $P < .001$; fig. 3A). However, there was a difference in the latitudinal clines between the two species (ANCOVA; species \times latitude interaction, $df = 1$, $F = 6.0$, $P < .05$; fig. 3B).

Geographic Variation in Ecological/Evolutionary Properties of the Interaction

The proportion of successful excavations varied widely among populations (17%–80%; table 2) and increased in more northern populations ($p_{SE} = -2.89 + 0.103 \times \text{latitude}$, $N = 15$, $df = 1$, $F = 18.6$, $P < .001$; fig. 4A). The proportion of infested seeds also had large interpopulation variation (0%–53%; table 2), although it did not show a significant latitudinal cline ($p_{IS} = -1.27 + 0.0456 \times \text{latitude}$, $N = 17$, $df = 1$, $F = 3.1$, $P = .10$); however, particularly severe infestation ($\approx 50\%$) was observed in several northern populations (fig. 4B).

In the 17 populations analyzed, the pericarp thickness of the Japanese camellia varied significantly among trees (nested ANOVA; $F_{\text{among populations}} = 52.8$, $df = 16, 255$, $P < .001$; $F_{\text{among trees}} = 12.7$, $df = 255, 435$, $P < .001$). In addition, the phenotypic variation in the defensive character was similar among populations (CV = 14%–32%; table 1). These results imply that, in all populations, there is interindividual variation potentially subject to natural selection. The standardized linear regression coefficient (β_o) varied widely among populations, from negative to positive, and increased at lower latitudes ($\beta_o = 1.65 - 0.0485 \times \text{latitude}$, $N = 17$, $df = 1$, $F = 5.9$, $P < .05$; fig.

Table 2: Geographic variation in the ecological/evolutionary properties of the interaction

Locality	Holes/fruit	p_{SE} (%)	p_{IS} (%)	Selection coefficients	
				β (SE)	γ (SE)
Kutsuki	22.7	74.2	46.1	-.131 (.156)	.348 (.258)
Kyoto	24.6	63.8	39.7	-.106 (.088)	.015 (.107)
Jurinji	31.6	80.2	52.9	-.074 (.109)	-.064 (.129)
Shodoshima	.28	-.004 (.003)	-.002 (.003)
Nara	12.2	72.4	39.0	-.081 (.051)	.005 (.069)
Kiikatsuura	11.6	73.1	32.1	.097 (.041)*	-.012 (.020)
Taiji	6.2	67.5	19.0	-.005 (.051)	.080 (.080)
Arafune	2.3	71.0	5.6	.015 (.029)	-.014 (.040)
Kiioshima	19.9	62.3	36.4	.047 (.070)	.101 (.096)
Muroto	7.0	53.6	20.0	-.063 (.033)	-.005 (.034)
Usa	6.5	46.5	7.9	.032 (.015)*	-.007 (.008)
Ashizuri	27.6	27.1	24.0	.046 (.019)*	.012 (.009)
Reihoku	46.6	28.7	32.0	.067 (.029)*	.039 (.018)*
Takahama	11.9	39.2	16.0	.064 (.013)**	-.012 (.008)
Ushibuka	.00	0	0
Yahazu	29.1	40.1	27.5	.044 (.017)*	.010 (.008)
Hanyama	20.1	16.8	15.3	.020 (.010)	.001 (.004)

Note: The average number of trial holes made by the camellia weevil per Japanese camellia fruit, the proportion of successful excavation (p_{SE}), and the proportion of infested seeds (p_{IS}) are shown for each population. Also, the results of linear/quadratic regressions, in which relative fitness of Japanese camellia (seed survival) was regressed on pericarp thickness, are presented.

* $P < .05$.

** $P < .0001$.

4C; table 2). In one locality (Reihoku), significant disruptive selection was detected by quadratic regression, while in other localities, the existence of stabilizing/disruptive selection remained obscure (table 2).

Discussion

For resolving the phenotypic interface of species interactions, the Japanese camellia–camellia weevil system provides a simple example. An experiment revealed the underlying mechanistic association between the pericarp thickness of the Japanese camellia and the rostrum length of the camellia weevil, and the inferred functional relationship enabled us to expect which species is at a relative advantage concerning phenotypic distribution in the respective populations. The geographic structure of the imbalance in armaments should result in variation in the proportion of successful excavations by the weevil, and it potentially affects the geographic heterogeneity of ecological/evolutionary processes of the plant–weevil interaction. In this sense, the severity of seed infestation and natural selection on the plant's defense were investigated in each population. The revealed geographic patterns illuminated the potential influence of the local balance between the traits of the interacting species on the geographic structuring of the outcome of the interactions.

Phenotypic Interface: Pericarp Thickness versus Rostrum Length

The interaction fitness function inferred from the experiment showed that the key characters of the two species, pericarp thickness and rostrum length, potentially played essential roles in the reproductive success of each species (seed survival and oviposition success, respectively; fig. 2G). With a thicker pericarp, the Japanese camellia can more successfully resist the attacks of the weevil, so individuals with a thicker pericarp would leave more seeds to future generations. Conversely, with a longer rostrum, the camellia weevil would have more chance to oviposit and should leave more offspring. In general, characters imposing major effects on the number of descendants should be favored by natural selection; hence, these defensive/offensive traits can evolve if they are heritable. Therefore, we suspect that evolutionary forces affect the pericarp thickness of the Japanese camellia and the rostrum length of the camellia weevil in the wild.

Correlation between Prey/Predator Traits across Populations

Both the pericarp thickness of the Japanese camellia and the rostrum length of the camellia weevil showed considerable variation among localities (table 1; fig. 3). The in-

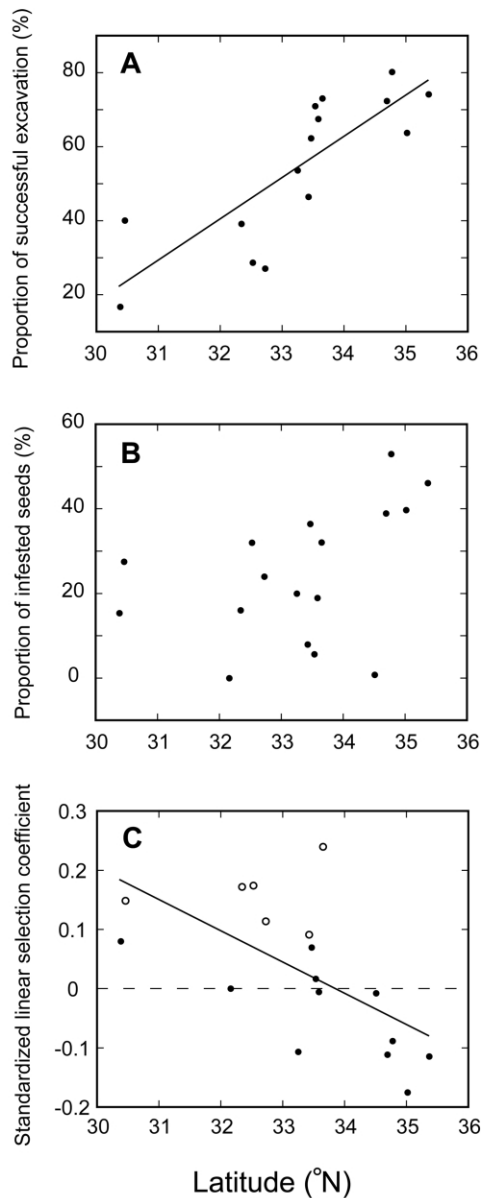


Figure 4: Latitudinal gradients in the ecological/evolutionary properties of the interaction. A, The proportion of successful excavations of the Japanese camellia pericarp by female camellia weevils. B, The proportion of seeds infested by weevil larvae. C, The standardized linear selection coefficient for the pericarp thickness of Japanese camellia. The open circles represent a significant association between phenotypes and relative fitness at $\alpha < 0.05$, whereas solid circles indicate nonsignificant ones (see table 2).

terpopulation variation in the predator and prey traits was two- or threefold at maximum. Given that there was a clear correlation between the defensive and offensive characters across the study sites (fig. 3), the interspecific in-

teraction between the two species should contribute to the geographic differentiation of those phenotypes.

Local matching between characters important for species interactions has already been reported in other plant-insect interactions (Carroll and Boyd 1992; Berenbaum and Zangerl 1998; Van Zandt 1998; Zangerl and Berenbaum 2003). In particular, Carroll and Boyd (1992) reported that the morphology of the soapberry bug (*Jadera haematoloma*) has undergone rapid differentiation between populations using native hosts and those using introduced hosts. Their native and introduced hosts differ in their fruit structure, and, as a result, the beak length of the soapberry bug has changed genetically in the predicted directions (Carroll and Boyd 1992; Carroll et al. 1997, 2003). Similarly, the camellia weevil would have undergone phenotypic differentiation in its mouthparts in response to the geographic variation in the defense of its host plant. Genetic, evolutionary change of traits involved in host use is potentially ubiquitous in insects (e.g., Carroll et al. 1997, 1998; Feder et al. 2003; Zangerl and Berenbaum 2003). Hence, in the case of the camellia weevil, the geographic variation in the trait that is highly specialized in excavating the pericarp of its obligate host plant may be attributed to selection imposed by the Japanese camellia. Further analyses are needed to assess the heritable variation in the weevil armament.

Note that remarkable geographic differentiation in both the plant's defense and the weevil's offense was observed between two populations separated by only 14 km. Analysis of the mitochondrial DNA sequence variation of the camellia weevil has verified that migration is restricted between the two populations (H. Toju and T. Sota, unpublished data), so local adaptation should have occurred on this small spatial scale, at least for the insect predator. These facts suggest that the evolutionary processes of prey and predator systems can be divided into a fine patchwork on geographic landscapes.

Local Imbalance between Prey/Predator Traits and Latitudinal Gradient in Interactions

We identified clear latitudinal clines for both the pericarp thickness of the Japanese camellia and the rostrum length of the camellia weevil (fig. 3B). However, there was a difference between the slopes of the two species. As a result, the balance in armaments was estimated to be relatively advantageous for the weevil in northern localities compared with southern ones (fig. 3). In fact, the weevil was more successful at penetrating the pericarp of the plant in more northern populations (fig. 4A).

Seed infestation was especially severe in several northern localities (fig. 4B). This may result from the geographic patterns in the proportion of successful excavations of the

pericarp by the camellia weevil, but other factors, such as the population density of the weevil, can also affect the severity of infestation. Given that prey under a higher predation risk generally evolve more developed defenses (Vermeij and Currey 1980; Bertness et al. 1981; Steinberg et al. 1995), the geographic variation in the intensity of infestation predicts that natural selection toward a thicker pericarp should be more evident in northern localities than in southern ones.

Nevertheless, counterintuitively, directional selection toward a thicker pericarp was more intense in more southern populations (fig. 4C). Because the direction and intensity of selection are determined by the association between fitness and focal traits (Price 1970; Lande and Arnold 1983; Arnold and Wade 1984), the geographic variation in directional selection suggests that pericarp thickness is more essential for seed survival in more southern localities. Given the geographic patterns in the imbalance between defensive/offensive armaments (fig. 3) and that in the proportion of successful excavations (fig. 4A), it seems that most Japanese camellia individuals in northern populations are too vulnerable to successfully defend their seeds against repeated attacks of the weevil predator (fig. 4A). Hence, in those populations, their seeds are infested independent of pericarp thickness, and there would be a weak correlation between traits and fitness. Note that in some northern populations, thinner pericarps were thought to be favored (table 2); our additional analysis revealed that fruits with a thicker pericarp had more trial holes made by the weevil females (H. Toju, unpublished data). This may reflect an oviposition preference of the females for large or early-growing fruit: the behavioral property of the weevil can also mediate the geographic differentiation of the defense of the Japanese camellia.

In the above analyses, we evaluated the potential effects of the imbalance between defensive/offensive armaments on the success of predator attacks, the intensity of seed infestation, and the local selection on the prey's defense. As such, the phenotypic distributions of species and sympatric participants are important determinants of local selection (Brodie and Brodie 1999; Brodie and Ridenhour 2003; Ridenhour 2005) and the geographic differentiation of the outcomes of interactions. One question remains to be resolved: why did the traits and the ecological/evolutionary properties of this system show latitudinal gradients? Given that climatic conditions and productivity change with latitude over our study sites (see Sota 1998 for geographic variation in litterfall amount in Japan), some environmental factors may affect the geographic differentiation of the interspecific interaction by, for example, altering the fecundity of hosts (Hochberg and van Baalen 1998) or the resource allocation costs of defensive/offensive traits (Saloniemi 1993; Sasaki and Godfray 1999).

Does an Arms Race Occur?

Although the geographic variation in the defensive/offensive traits and the consistent pattern in natural selection on the defense of the Japanese camellia are consistent with the hypothesis of coevolutionary arms races (Dawkins and Krebs 1979), we are unsure whether reciprocal selection is ongoing in this system. Characters apparently adapted to species interactions may have another major function (Rausher 2001) or they may simply be affected by non-adaptive factors; therefore, alternative explanations might be possible for the geographic variation in pericarp thickness other than the occurrence of coevolution. For example, the latitudinal cline in pericarp thickness might result from phenotypic plasticity expressed along productivity gradients, and the camellia weevil might just be tracking the geographic variation in Japanese camellia. However, it is probable that the pericarp thickness of this plant is determined genetically, because genetic variation in fruit size or pericarp thickness has been demonstrated in different commercial cultivars of some congeners of Japanese camellia, such as tea (*Camellia sinensis*; International Plant Genetic Resources Institute 1997) and tea oil camellia (*Camellia oleifera*; Fang 1997). Furthermore, a breeding line of Japanese camellia that has been selected to increase the production of seed oil gained much larger fruit size (S. Yamaguchi, personal communication). Consequently, the geographic variation in the fruit character may be the product of locally varying selection, presumably attributable to infestation by the camellia weevil (fig. 4C).

Possible adaptive functions other than defense against the camellia weevil can be raised for the fruit character. A thick pericarp might have evolved in order to protect maturing seeds from desiccation or cold/frost damage. However, a closely related sympatric species, *Camellia sasanqua*, has a much thinner pericarp (≈ 2 mm) than that of the Japanese camellia (6–20 mm on average; table 1). This seems to suggest that a 2-mm-thick pericarp is sufficient for the physical environmental conditions.

Natural enemies other than the camellia weevil might influence pericarp evolution. An unidentified fungus species parasitizes the Japanese camellia fruit, but the infection seems to occur in flower season or early fruit development because fungal tissue is observed early in the growing season of the plant fruit (H. Toju, personal observation). Hence, the pericarp thickness would not be related to the interaction with this fungus. The Japanese macaque (*Macaca fuscata*) occasionally bites fruit of the Japanese camellia, but most of the attacked fruit has already been parasitized by the fungus (M. Nishikawa, personal communication). Hence, the selective impact of this monkey on pericarp thickness should be negligible. Therefore,

those biotic factors presumably have not been the major selective agents for the thick pericarp of the Japanese camellia. Indirect effects of other traits or genes, such as pleiotropy or close linkage, potentially affect pericarp thickness (Rausher 2001), and these possibilities should be examined in future investigations. Overall, although the potential impact of the above-mentioned factors should not be neglected, the occurrence of geographically structured coevolution with the camellia weevil seems to be the most plausible explanation for the remarkable phenotypic differentiation in the pericarp thickness of the Japanese camellia.

Conclusion

In this study we showed that the phenotypic interface between prey and predator armaments could vary dramatically among populations. In addition, it is suggested that the imbalance in armaments between sympatric prey and predator affects local selection on prey (and potentially that on the predator), and as a consequence, the process of coevolutionary arms races could be structured across geographic landscapes. Another important implication arising from our study is that the escalation in armaments may be accelerated in populations at lower latitudes. It is widely known that the arms of prey and predator are more exaggerated in tropic than in temperate regions; but the causes of the pattern are controversial (Vermeij 1978; Vermeij and Currey 1980; Bertness et al. 1981). Further investigations are needed to reveal the factors regulating or promoting coevolution in local populations and thereby causing geographic differentiation of interspecific interactions.

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