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「魚類群集における反対称捕食の維持機構の数理生態学的
研究」

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研究成果報告書

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研究成果の概要

多くの魚類に右利きと左利きの遺伝的 2 形があり、捕食者が自分とは利きの違うほうの被食者を食べることによって維持されることを室内実験、野外標本の胃内容物調査、および数理モデルにより検証した。数理モデルによる検証により、雑食性（ギルド内捕食、最上位捕食者が中位捕食者だけでなく、最下位の餌生物も直接捕食すること）がある場合には右利きと左利きが共存しつつも、頻度が必ず振動することを明らかにした。これにより、異なる利きの被食者を食べるのが新たな概念として学界で認められた (Nakajima, Matsuda, Hori 2004: American Naturalist)。ただし、名称は反対称捕食ではなく、cross predation (交差捕食と訳出) として認められた。すなわち、「捕食関係を通じた頻度依存淘汰という新しい分断性非対称の維持機構を新たな概念として定式化する」という「本研究の第一の目的」、ならびに「雑食が左右二型の頻度の安定性にどう寄与するかを明らかにする」という第 2 の目的を果たした。

さらに、遺伝的浮動のある集団遺伝モデルによる解析も行った (Nakajima, Masuda, Hori 印刷中)。また、室内実験ならびに胃内容物調査から、魚食性の魚の場合には交差捕食が 100%ではなく、並行捕食（捕食者と被食者の危機が同じもの）が 1/4 程度含まれる例も明らかになった。さらに、利きの程度を定量化する試みもブラックバスなどを用いて進めており、左右性の進化に関わるモデル作りを継続して進めている。

キーワード 分断非対称性、交差捕食、魚類、数理モデル、周期変動、雑食

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- [A67x] Matsuda H (2005) How to test and apply ecological models to fisheries management of sardine and other pelagic fishes. Progress in Oceanography in press
- [A64x] Nakajima M, Matsuda H, Hori M (2005) A Population Genetic Model for Lateral Dimorphism Frequency in Fishes. Pop Ecol in press:
- [A62x] Abrams PA, Matsuda H (2005) The effect of adaptive change in the prey on the dynamics of an exploited predator population. Can J Fish Aq Sci in press:
- [A59] Abrams PA, Matsuda H (2004) Consequences of behavioral dynamics for the population dynamics of predator-prey systems with switching. Pop Ecol 46: 13-25
- [A58] Nakajima M, Matsuda H, Hori M (2004) Persistence and fluctuation of lateral dimorphism of fishes. Am Nat 163:692-698
- [A57] Matsuda H, Abrams PA (2004) Effects of predator-prey interactions and adaptive change on sustainable yield. Can J Fish Aq Sci 61:175-184
- [B18x] Nakajima M, Matsuda H, Hori M (2004) Role of omnivory for fluctuation of lateral dimorphism in fishes. Biology International, in press
- [E19] 松田裕之(2004) ゼロからわかる生態学, 環境, 進化, 持続可能性の科学. 共立出版

Persistence and Fluctuation of Lateral Dimorphism in Fishes

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ABSTRACT: Two morphological types ("righty" and "lefty") have been discovered in several fish species and are referred to as a typical example of antisymmetry. It has been suggested, first, that this dimorphism (called laterality) is inheritable; second, that the frequencies of laterality in each species fluctuate around 0.5; and third, that predators mainly exploit prey of the opposite laterality; that is, lefty and righty predators prey on righties and lefties, respectively. The latter is defined as "cross predation"; the antonym "parallel predation" means predation within the same laterality. We hypothesized that cross predation drives alternation of the survival and reproductive advantages between two morphological types, leading to frequency-dependent selection that maintains the dimorphism. To investigate this, we constructed mathematical models of population dynamics of one prey/one predator systems and three-trophic-level systems with omnivory. Mathematical analysis and computer simulations explained the behavior of the laterality frequency in nature well, insofar as cross predation dominated over parallel predation. Furthermore, the simulations showed that when only one of the morphological types exists in a species, the other type can invade. This suggests that dimorphism is maintained in all interacting species.

Keywords: laterality, antisymmetry, prey-predator system, omnivory, dimorphism, frequency-dependent selection.

Although one of the factors known to maintain polymorphism is frequency-dependent selection, this has not

been clearly demonstrated in field data. Hori (1991, 1993) found two morphological types in a population of scale-eating cichlids *Perissodus microlepis* in Lake Tanganyika: one type has its mouth opening to the right, causing the left side of its head to more or less face the front (termed "lefty"), while the other type has its mouth to the left, causing the right side of the head to face forward ("righty"). Note that Hori (M. Hori, unpublished manuscript) has changed the definitions of lefty and righty to those described above; in previous works (Hori 1991, 1993), he considered an individual with its mouth opening to the left to be "left-handed" or "sinistral." As Mboko et al. (1998) and Seki et al. (2000) mentioned, this asymmetry in laterality differs from fluctuating asymmetry (see the definition in Van Valen 1962) in that there are no "middle" or "normal" individuals with little deviation from symmetry. It is a typical example of "antisymmetry" (Palmer 1996), which has a bimodal distribution of signed differences on both sides (Van Valen 1962).

Hori (1991, 1993) has described several features of this type of dimorphism. First, the laterality is inheritable in a Mendelian one locus/two allele fashion, with lefties dominating; second, the proportion of lefties in the population over 11 yr showed a periodical oscillation around 0.5; and third, lefty scale eaters in Lake Tanganyika attacked only the left flanks of their prey, whereas righty scale eaters attacked only the right flanks of prey. Recently, laterality has been found not only in populations of the scale eaters *P. microlepis* and *Perissodus straeleni* (Hori 1993, 2000; Takahashi and Hori 1998) but also in other Lake Tanganyika cichlids (*Telmatochromis temporalis*; Mboko et al. 1998; 19 other species; M. Hori, unpublished manuscript) and even in a freshwater goby *Rhinogobius flumineus* in a Japanese river (Seki et al. 2000). In addition, laterality appears in both prey and predator fish species, and predators usually attack prey of the opposite morphological type (Hori 2000). Here we define "cross predation" as predation when predators exploit prey of the opposite laterality, that is, when lefties and righties of the same predator species feed on righties and lefties, respectively, of the prey species. Conversely, we define "parallel predation" as a situation in which predators feed on prey of the same laterality. To explain the mechanism that main-

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Table 1: Equilibria of models 1 and 2

y^*	$= r[(C_{yz} + P_{yz})Km - d_y] / (C_{yz} + P_{yz})^2 Km$
z^*	$= d_y / (C_{yz} + P_{yz}) m$
x^*	$= r[(C_{xz} + P_{xz})Km - d_x] / (C_{xz} + P_{xz})^2 Km$
z^*	$= d_x / (C_{xz} + P_{xz}) m$
x^*	$= \frac{(C_{yz} + P_{yz})K[(C_{xz} + P_{xz})d_y + (C_{xy} + P_{xy})mr - (C_{yz} + P_{yz})d_x] - (C_{xy} + P_{xy})d_y r}{(C_{xy} + P_{xy})[(C_{xy} + P_{xy})r - (C_{xz} + P_{xz})(C_{yz} + P_{yz})K(1 - m)]}$
y^*	$= \frac{(C_{xz} + P_{xz})Km[(C_{yz} + P_{yz})d_x - (C_{xy} + P_{xy})r - (C_{xz} + P_{xz})d_y] + (C_{xy} + P_{xy})d_x r}{(C_{xy} + P_{xy})m[(C_{xy} + P_{xy})r - (C_{xz} + P_{xz})(C_{yz} + P_{yz})K(1 - m)]}$
z^*	$= \frac{K[(C_{xy} + P_{xy})mr + (C_{xz} + P_{xz})d_y m - (C_{yz} + P_{yz})d_x]}{m[(C_{xy} + P_{xy})r - (C_{xz} + P_{xz})(C_{yz} + P_{yz})K(1 - m)]}$

tains laterality with oscillations of phenotype frequencies in the population, Hori (1993) proposed that prey might focus their vigilance toward the left or right flank when lefty or righty predators are abundant.

Matsuda et al. (1993, 1994, 1996) argued that predator-specific defense provides an advantage to less abundant phenotypes that attack the unguarded flanks. A minority advantage in laterality among predators will result in increased reproductive success, which will make this type dominant in the future (Sih et al. 1998). In addition, Saleem et al. (2003) suggested that this switching of vigilance can generally stabilize one prey/two predator systems. This predator-specific defense also maintains polymorphism among predators (Takahashi and Hori 1994). Therefore, laterality has been referred to as one of the most typical examples of frequency-dependent selection (Lively 1993; Bulmer 1994). Of note, observations of several species have suggested that the direction of immediate movement (e.g., attacking and fleeing) depends on laterality (M. Hori, unpublished manuscript). Righties tend to dash to the left, while lefties move to the right. Therefore, prey availability might depend on the laterality of prey and predators. Lateral antisymmetry in these fishes might be a widespread feature of predation.

We would expect that cross predation would lead to the transition of survival and reproductive advantages between the two types; when lefty dominates in a predator species, righty prey would decrease, and then, automatically, lefties would become dominant in a prey species, followed by domination of righties in a predator species. To investigate this hypothesis, first we introduce a mathematical model of a simple one prey/one predator system, and later we expand this model to a more complicated food web. Although several studies have indicated that antisymmetry is important in sexual selection (Rowe et al. 1997; Pope 2000; Pratt and McLain 2002), no investigation has considered predation.

Model 1: One Predator/One Prey System

This food web includes a predator species y and prey species z . We assumed that fish reproduce asexually and that laterality is inheritable. We denote the population sizes of lefties and righties of species y and z by y_L and y_R and z_L and z_R , respectively. Because laterality is considered anti-symmetric, the rates of growth, predation, and death must be symmetric between lefties and righties. The dynamics of two species were described with linear functional response:

$$\frac{dy_R}{dt} = [m(C_{yz}z_L + P_{yz}z_R) - d_y]y_R, \tag{1a}$$

$$\frac{dy_L}{dt} = [m(C_{yz}z_R + P_{yz}z_L) - d_y]y_L, \tag{1b}$$

$$\frac{dz_R}{dt} = \left[r \left(1 - \frac{z_R + z_L}{K} \right) - C_{yz}y_L - P_{yz}y_R \right] z_R, \tag{1c}$$

$$\frac{dz_L}{dt} = \left[r \left(1 - \frac{z_R + z_L}{K} \right) - C_{yz}y_R - P_{yz}y_L \right] z_L, \tag{1d}$$

where $C_{ij} (\geq 0)$ and $P_{ij} (\geq 0)$ are the efficiencies of predation when predator i preys on prey j with the opposite (i.e., cross predation) or the same (i.e., parallel predation) laterality, respectively; $m (\leq 1)$ is the metabolic rate; $d_y (\leq 1)$ is the death rate of the predator; and $r (>0)$ and $K (>0)$ are the intrinsic rate of population increase and the carrying capacity of the prey species, respectively. We assume that the rates of population increase of z_L and z_R depend on the total population size of the prey. This assumption is biologically reasonable while lefty and righty prey use the same habitat or other resources.

This system has an equilibrium $(y_L, y_R, z_L, z_R) = (y^*, y^*, z^*, z^*)$ at which all four populations coexist (see table 1; app. A in the online edition of the *American Naturalist*

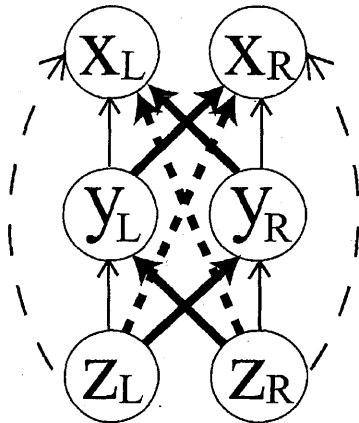


Figure 1: Diagram of a three-trophic-level food web with lefties (left) and righties (right) of species x , y , and z . Arrows indicate the directions of food intake (thick arrows, cross predation; thin arrows, parallel predation). When the top predator is omnivorous, dashed arrows indicate intake from z to x .

for details). We confirm the global stability of this two-species system at this equilibrium in appendix A, using a Lyapunov function. The linearized system surrounding the equilibrium has a neutrally stable equilibrium (see app. A). Computer simulations took too long for any trajectories to reach equilibrium and showed periodic oscillations of laterality frequencies in both prey and predator that were similar to field observations conducted in Lake Tanganyika (Hori 1993, 2000). They agreed with our hypothesis of the transition of survival and reproductive advantages between the two types.

Model 2: Three-Trophic-Level System

Next, we added a top predator species x , which consumes species y , to the former y - z food web. We describe righties and lefties of x as x_R and x_L . As one would expect, the influence of cross predation is similar to the former model of equations (1); when x_R dominates in species x , y_L would decrease, and hence y_R would dominate automatically, followed by the decrease of its prey, z_L . Again, the simulations took too long for any trajectories to reach this equilibrium. The Lyapunov function showed that this system is globally stable (see app. A for details).

The story is more complicated when the top predator x also preys on the bottom prey z because this omnivory of species x imposes contradictory selective pressures on the bottom trophic level (fig. 1). Here "omnivory" is defined as the feeding on nonadjacent trophic levels (Pimm and Lawton 1978; Pimm 1982). In this food web, when

lefties dominate in bottom prey species, righty consumers have an advantage, which in turn conveys an advantage to lefty top predators. If we consider predation on the bottom prey by the top predator (shown by the dashed arrows in fig. 1), however, righties dominate among the top predator when lefties dominate among the bottom prey. Although it is possible to think that the fitnesses of both righties and lefties are equal in the top predator, observations of oscillating frequencies of righties suggest that advantages are alternately conferred between the two phenotypes (Hori 1991, 1993). To investigate how this transition in advantages among the top predators occurs in the wild, we investigated a mathematical model that has an additional omnivory term.

This three-trophic food web with omnivory was introduced by Holt and Polis (1997). This kind of food web exists among the cichlids in Lake Tanganyika (Hori 1987, 1997), and oscillation in the frequency of the righty phenotype has been observed at each trophic level (Seki et al. 2000; M. Hori, unpublished manuscript). With reference to this food web, the scale eater is considered the top predator (x), piscivores are intermediate predators (y), and algal feeders are the bottom prey (z). The frequency dynamics of each laterality of this food web are given as

$$\frac{dx_R}{dt} = [m(C_{xy}y_L + P_{xy}y_R + C_{xz}z_L + P_{xz}z_R) - d_x]x_R \tag{2a}$$

$$\frac{dx_L}{dt} = [m(C_{xy}y_R + P_{xy}y_L + C_{xz}z_R + P_{xz}z_L) - d_x]x_L \tag{2b}$$

$$\frac{dy_R}{dt} = [m(C_{yz}z_L + P_{yz}z_R) - C_{xy}x_L - P_{xy}x_R - d_y]y_R \tag{2c}$$

$$\frac{dy_L}{dt} = [m(C_{yz}z_R + P_{yz}z_L) - C_{xy}x_R - P_{xy}x_L - d_y]y_L \tag{2d}$$

$$\frac{dz_R}{dt} = \left[r \left(1 - \frac{z_R + z_L}{K} \right) - C_{xz}x_L - P_{xz}x_R - C_{yz}y_L - P_{yz}y_R \right] z_R \tag{2e}$$

$$\frac{dz_L}{dt} = \left[r \left(1 - \frac{z_R + z_L}{K} \right) - C_{xz}x_R - P_{xz}x_L - C_{yz}y_R - P_{yz}y_L \right] z_L \tag{2f}$$

where d_x (≤ 1) is the death rate of the top predator and the other parameters are the same as in equations (1). Note that equations (2) are equal to equations (1) when $x_R = x_L = 0$. We should also mention that the system loses omnivory when $C_{xz} = P_{xz} = 0$.

We describe $x_R, x_L, y_R, y_L, z_R, z_L$ as a vector $E = (x_R, x_L, y_R, y_L, z_R, z_L)$. There are four equilibria that consist of equal populations of both types in each species: first, the top and intermediate predators become extinct, denoted by $E^0 = (0, 0, 0, 0, z_R^0, K - z_R^0)$; second, the top predator becomes extinct, $E^1 = (0, 0, y^+, y^+, z^+, z^+)$; third, the intermediate predator becomes extinct, $E^2 = (x^+, x^+, 0, 0,$

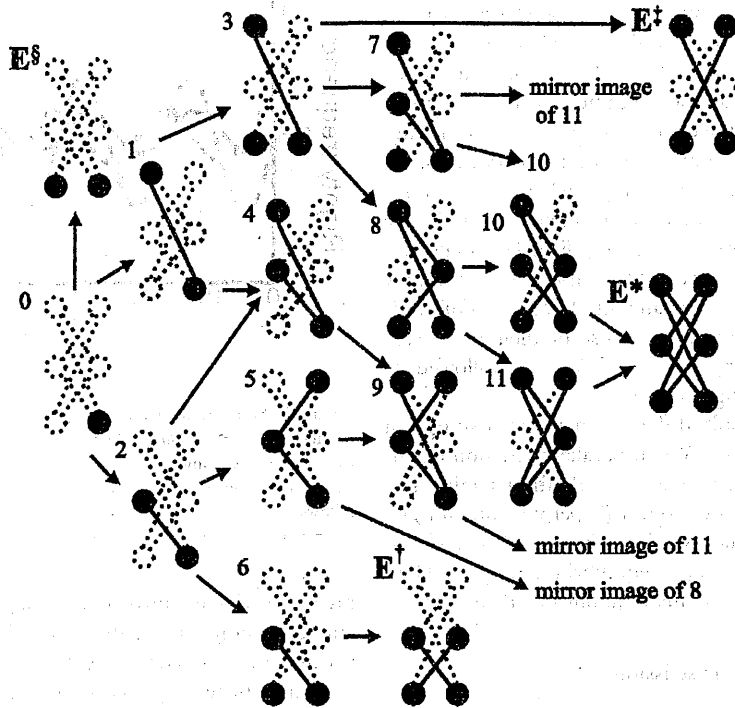


Figure 2: Sixteen out of 33 equilibria for equations (2). Each circle in an equilibrium indicates each of the six populations, that is, lefties (left) and righties (right) of all three species (bottom, z; middle, y; top, x). Lines indicate cross predation. In equilibria 0–11 that contain monomorphic species, the other laterality can invade the system, which changes the food web structure in the direction of the arrows. We have not shown the other 18 equilibria that involve parallel predation only (for example, invasion of y_R to equilibrium 0) to avoid congestion. We omitted the mirror images of food webs 0–11.

z^\dagger, z^*); and fourth, the three species coexist, $E^* = (x^*, x^*, y^*, y^*, z^*, z^*)$, where $y^\dagger, z^\dagger, x^\dagger, z^\dagger, x^*, y^*$, and z^* are given by equations in table 1. Note that equilibrium E^\dagger is equal to the equilibrium of equations (1).

The population size of righty and lefty in a species differs in 28 other equilibria in model 2. We show the principal ones in figure 2. These and one trivial equilibrium (0, 0, 0, 0, 0, 0) are invadable by other species or types of species; thus, the system converges on the symmetric equilibrium, that is, E^s, E^\dagger, E^* , or E^* . Figure 2 illustrates which population can invade which equilibrium if equilibrium exists. For example, because we assume that foraging ability, mortality, and fecundity are identical between lefties and righties, on the basis of field observations by Hori (1993), it is clear that a righty top predator can invade the equilibrium (0, $x_L, 0, 0, z_R, z_L$), that is, equilibrium 3 in figure 2, and the system may transit to equilibrium E^\dagger after invasion. As another example, an asymmetric equilibrium $E^\dagger = (0, x^#, y^#, 0, z_1^#, z_2^#)$, that is, equilibrium 8 in figure 2, might be misunderstood as the finish at first glance. Lefties and righties are included in both predators and

prey, although each of the two predator species holds either laterality. We investigated two aspects of the stability of this equilibrium: first, whether the absent type in species x or y invades equilibrium E^\dagger , that is, whether $(dx_R/dt)/x_R > 0$ or $(dy_L/dt)/y_L > 0$ are satisfied at E^\dagger , and second, whether this equilibrium is locally stable for any perturbation of existing populations, x_L, y_R, z_R , and z_L . In the numerical analysis, either one of the invadability inequalities is satisfied whenever E^\dagger is locally stable if the efficiency of cross predation exceeds that of parallel predation ($C_{ij} > P_{ij}$), as shown in appendix B in the online edition of the *American Naturalist*. Therefore, this asymmetric equilibrium is not maintained but moves to another state (equilibrium 10 or 11 in fig. 2) at that time. We also note that the invadability graph (fig. 2) has no cycles that allow a return to the asymmetric equilibrium from the symmetric, dimorphic one.

We examined the dynamic behavior of six populations (eqq. [2]) using computer simulations because the equilibrium $E^* = (x_R^*, x_L^*, y_R^*, y_L^*, z_R^*, z_L^*)$ is complex and difficult to analyze mathematically. With many parameter sets

of various values of predation efficiencies, the frequencies of laterality in each population fluctuated significantly; they converged on periodic oscillations (fig. 3) in a manner similar to field data (Hori 1993; M. unpublished manuscript) as long as no species became extinct. The simulations described well the coexistence of lefties and righties in all three species on a limit cycle. If omnivory exists, the dynamics of three species are unstable when the total population sizes of each species are constant (app. C in the online edition of the *American Naturalist*). The oscillation of each of the three species had the same period, but they were not synchronized. The laterality frequencies of predators were always followed by those of their prey (e.g., x_R and y_R followed $z_L (= 1 - z_R)$, and x_R followed $y_L (= 1 - y_R)$ and z_L in fig. 3).

The simulation result differed when the assumption $C_{ij} > P_{ij}$ was not satisfied. When parallel predation dominates in all predators, that is, $C_{ij} < P_{ij}$, the laterality frequencies did not oscillate around E^* permanently for any of the parameter values we investigated; it changed to various monomorphic states (equilibrium 8, 10, or 11 in fig. 2) or two-species systems (equilibrium E^+ or E^*).

Discussion

This work shows the importance of lateral antisymmetry and cross predation in maintaining two morphological types, which leads to alternation in the survival and reproductive advantages of the two types. Antisymmetry enabled us to set symmetric parameter values for lefties and righties. Such symmetry simplifies the mathematics and lets the minority advantage alter equally, increasing the possibility of coexistence, as compared with population models that include six monomorphic species. Under frequency-dependent selection for lateral dimorphism, the lefty predator has a selective advantage over the righty when the former's resource (righty prey) is more abundant and vice versa. This is to be expected because each morphological type has common ecological parameters. Because the prey abundance again depends on the predator's density, it is very unlikely that either laterality dominates permanently. It is also notable that the frequency-dependent selection for lateral dimorphism has a time lag because the response of the predator to an increase in its prey is delayed. Our simulation supported the idea that the lateral frequencies of prey and predator oscillated but were not synchronized as in prey-predator cycles.

In the computer simulations of model 2, the frequency of a morphological type among predators always oscillated; moreover, the frequency of a morphological type in both predator species followed that of their major prey, that is, prey of the opposite laterality (fig. 3). This is in contrast to the peak in predator density that follows the peak in

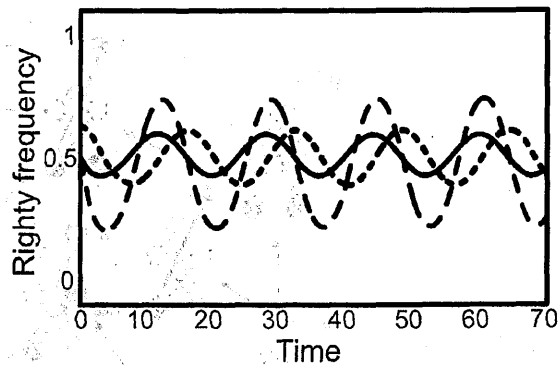


Figure 3: Simulation of the population dynamics (eqq. [2]) of three species (solid line, x_R ; dashed line, y_R ; and dotted line, z_R). We obtain the trajectory using numerical calculations of Euler's approximation of difference equations with the time step $\Delta t = 0.001$. Parameters used are as follows: $C_{yz} = 1.0$, $P_{yz} = 0.15$, $C_{xz} = 0.3$, $P_{xz} = 0.0525$, $C_{xy} = 0.6$, $P_{xy} = 0.4$, $m = 0.8$, $d_x = d_y = 0.5$, $K = 10$, and $r = 1$.

prey densities in most models of homogenous predator and prey populations that cycle. This is not surprising because righty predators feed mainly on lefty prey, consequently benefiting righty prey. In addition, the intermediate predator, y , was always delayed in comparison with the top predator, x , in our computer simulations (fig. 3). This delay must be due to omnivory by the top predator because an increase in x_R might have a great impact on the population size of its prey, y_L , enough to reduce the response to the increase in the prey of y_L , that is, z_R . The impact must also be strong enough to reduce the advantage of y_L , which has few competitors (x_L) for the common prey (z_R). Hence, y_R continued to increase even after its prey started to decrease because its predator had less of an impact. In the simulation, excessive values made the six-population system unstable, which led to the extinction of some populations.

The results of computer simulations in which the efficiency of cross predation was less frequent than that of parallel predation, that is, $C_{ij} < P_{ij}$, differed from those with $C_{ij} > P_{ij}$ and/or the observed data for Lake Tanganyika. With the unnatural assumption $C_{ij} < P_{ij}$, when the lefty dominates in z , y_L has the advantage and so, too, does x_L , which prey on both z_L and y_L . Therefore, the opposite selective pressure on the bottom prey from the omnivorous top predator dissolves at this time. This confirmed the idea that especially in three-trophic-level food webs with omnivory, cross predation causes a transition in the advantage between righties and lefties, which in turn causes the persistence and fluctuation of dimorphism.

Note that our models include two or three species that have both morphological types, lefty and righty, although

coexistence and oscillation in the frequencies of laterality of all species have been observed in fish communities in Lake Tanganyika (M. Hori, unpublished manuscript). It is not clear whether the monomorphic state (e.g., all individuals are lefty) is always unstable for some species in more complex food webs. In addition, we have not yet examined the oscillation and coexistence of dimorphism in food webs containing more than three species. To examine interspecific or interguild relationships in laterality, continuous field observations of a multispecies food web (e.g., in Lake Tanganyika; Hori 1997) are required.

Here we have shown a very simple model describing the basic ecology of lateral antisymmetry, which, in nature, would be more complicated. By way of realizing such complexity, we attempted to adopt a nonlinear, Type II, functional response that contains the handling time of predation (see Murdoch and Oaten 1975; Hofbauer and Sigmund 1998). The parameter range of species extinction was larger than that of the linear functional response models (M. Nakajima, H. Matsuda, and M. Hori, unpublished manuscript). In addition, we simulated models including demographic stochasticity. The results did not change significantly from those in figure 3, although the oscillations were serrated and not perfectly periodic (M. Nakajima, H. Matsuda, and M. Hori, unpublished manuscript). The model could be expanded when the detailed ecology and inheritance of laterality are revealed to make it more realistic; this might result in new findings. Several problems with laterality remain unresolved: the influence of antisymmetry on interactions other than predation, for example, competition and mating; the influence of the magnitude of laterality between and within species; and the origin of antisymmetry in laterality and how it is inherited. We need to explore effective sampling methods or devise practical experiments that will illuminate the mechanism in nature.

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Online Appendix

Online Appendix A: Stability of the y-z Community and 3-trophic-level system

Equilibrium \mathbf{E}^\dagger exists when $(C_{yz} + P_{yz})Km - 2d_y > 0$. The Jacobian matrix used for the local stability analysis of $(y_L, y_R, z_L, z_R) = (y^\dagger, y^\dagger, z^\dagger, z^\dagger)$ in Model 1 is:

$$\begin{bmatrix} \frac{\partial}{\partial y_R} \frac{dy_R}{dt} & \frac{\partial}{\partial y_L} \frac{dy_R}{dt} & \frac{\partial}{\partial z_R} \frac{dy_R}{dt} & \frac{\partial}{\partial z_L} \frac{dy_R}{dt} \\ \frac{\partial}{\partial y_R} \frac{dy_L}{dt} & \frac{\partial}{\partial y_L} \frac{dy_L}{dt} & \frac{\partial}{\partial z_R} \frac{dy_L}{dt} & \frac{\partial}{\partial z_L} \frac{dy_L}{dt} \\ \frac{\partial}{\partial y_R} \frac{dz_R}{dt} & \frac{\partial}{\partial y_L} \frac{dz_R}{dt} & \frac{\partial}{\partial z_R} \frac{dz_R}{dt} & \frac{\partial}{\partial z_L} \frac{dz_R}{dt} \\ \frac{\partial}{\partial y_R} \frac{dz_L}{dt} & \frac{\partial}{\partial y_L} \frac{dz_L}{dt} & \frac{\partial}{\partial z_R} \frac{dz_L}{dt} & \frac{\partial}{\partial z_L} \frac{dz_L}{dt} \end{bmatrix}_* \quad (\text{A1})$$

where an asterisk indicates that partial derivatives are taken at the equilibrium \mathbf{E}^\dagger .

Then the eigenvalues of this Jacobian matrix are:

$$\sqrt{\frac{(C_{yz} - P_{yz})^2 E d_{y,r}}{-(C_{yz} + P_{yz})^3 Km}} \quad , \quad -\sqrt{\frac{(C_{yz} - P_{yz})^2 E d_{y,r}}{-(C_{yz} + P_{yz})^3 Km}} \quad , \quad (\text{A2A,B})$$

where $E = (C_{yz} + P_{yz})Km - 2d_y$. This equilibrium exists when $E > 0$. The eigenvalues (A2A, B) are always purely imaginary.

To analyze the global stability of this 2-species system, we introduce a Lyapunov function, L_1 (see Nisbet and Gurney 1982 for a detailed explanation). We set $m = 1$, which does not cause a loss of generality for this model. We define L_1 as:

$$\begin{aligned} L_1 = & y^\dagger [y_R / y^\dagger - 1 - \log(y_R / y^\dagger)] + y^\dagger [y_L / y^\dagger - 1 - \log(y_L / y^\dagger)] + \\ & z^\dagger [z_L / z^\dagger - 1 - \log(z_L / z^\dagger)] + z^\dagger [z_R / z^\dagger - 1 - \log(z_R / z^\dagger)] \end{aligned} \quad (\text{A3})$$

where $L_1 \geq 0$ for any point (y_R, y_L, z_R, z_L are positive) and equality must hold at equilibrium. We should note that:

$$\frac{dL_1}{dt} = -\frac{r \left[(C_{yz} + P_{yz})(z_L + z_R) - 2d_y \right]^2}{(C_{yz} + P_{yz})^2 K}, \quad (\text{A4})$$

$dL_1/dt \leq 0$ for any point, and equality holds at $(z_L + z_R) = 2d_y/(C_{yz} + P_{yz})$. Therefore, no population diverges. The total prey population ($z_L + z_R$) changes when $(z_L + z_R) = 2d_y/(C_{yz} + P_{yz})$, except at equilibrium. Therefore, this system is globally stable.

The dynamics of a 3-trophic-level system without omnivory (substituting $C_{xz} = P_{xz} = 0$ into Eq. 2) has a Lyapunov function as the y-z system when $m = 1$:

$$\begin{aligned} L_2 = & x^* [x_R/x^* - 1 - \log(x_R/y^*)] + x^* [x_L/x^* - 1 - \log(x_L/x^*)] + \\ & y^* [y_R/y^* - 1 - \log(y_R/y^*)] + y^* [y_L/y^* - 1 - \log(y_L/y^*)] + \\ & z^* [z_L/z^* - 1 - \log(z_L/z^*)] + z^* [z_R/z^* - 1 - \log(z_R/z^*)], \end{aligned} \quad (\text{A5})$$

$$\frac{dL_2}{dt} = -\frac{\left[(C_{yz} + P_{yz})d_x K + (C_{xy} + P_{xy})(z_R + z_L - K)r \right]^2}{(C_{xy} + P_{xy})^2 Kr}, \quad (\text{A6})$$

$L_2 \geq 0$ and $dL_2/dt \leq 0$ at any point, and the equalities hold at the equilibrium E^* (details of the equilibrium are in Table 1, substituting $C_{xz} = P_{xz} = 0$ into E^*). We should mention that this function is not applicable to the omnivorous model (Eq. 2) if $m < 1$.

Online Appendix B: Invadability of the 3-Trophic-Level System $E^\#$ by Lefties and Righties

Equilibrium $E^\#$ can be written as:

$$x^\# = r(C_{yz} - P_{yz}) \left[(C_{xz}C_{yz} - P_{xz}P_{yz})Km - d_x(C_{yz} - P_{yz}) - d_y(C_{xz} - P_{xz}) \right] / D,$$

$$\begin{aligned}
y^\# &= r(C_{xz} - P_{xz})[(C_{xz}C_{yz} - P_{xz}P_{yz})Km - d_x(C_{yz} - P_{yz}) - d_y(C_{xz} - P_{xz})]/D, \\
z_1^\# &= \{C_{xz}C_{yz}Km[-P_{xz}d_y + C_{yz}d_x - C_{xy}mr] + P_{xz}P_{yz}Km[P_{xz}d_y - C_{yz}d_x + C_{xy}r] \\
&\quad + (C_{xz} - P_{xz})C_{xy}d_ymr + (C_{yz} - P_{yz})C_{xy}d_xr - C_{xy}P_{xz}C_{yz}Kmr(1-m)\}/mD, \\
z_2^\# &= \{C_{xz}C_{yz}Km[C_{xz}d_y - P_{yz}d_x + C_{xy}r] + P_{xz}P_{yz}Km[-C_{xz}d_y + C_{yz}d_x - C_{xy}mr] \\
&\quad - (C_{xz} - P_{xz})C_{xy}d_ymr - (C_{yz} - P_{yz})C_{xy}d_xr - C_{xy}C_{xz}P_{yz}Kmr(1-m)\}/mD,
\end{aligned} \tag{A7}$$

where

$$D = (C_{xz}C_{yz} - P_{xz}P_{yz})^2 Km + C_{xy}r(1-m)(C_{xz} - P_{xz})(C_{yz} - P_{yz}).$$

Note that $D > 0$ when $C_{xz} > P_{xz}$ and $C_{yz} > P_{yz}$. This equilibrium exists when all $x^\#, y^\#, z_1^\#$ and $z_2^\#$ take positive values. Either of the absent type in species x or y can invade equilibrium $\mathbf{E}^\#$ when $(dx_L/dt)/x_L > 0$ or $(dx_R/dt)/x_R > 0$ at $\mathbf{E}^\#$, respectively. Therefore, this asymmetric equilibrium is not maintained, but may move to another state (equilibrium 10 or 11 in Fig. 2). Note that when predators mainly attacked prey of the same laterality ($P_{ij} > C_{ij}$) this equilibrium was locally stable and was uninvadable for certain parameter sets. This is not surprising because the main prey of the two predators do not overlap.

Online Appendix C:

Linear Stability Analysis of 3 Species Dynamics of Laterality Frequencies

Since the equilibrium $\mathbf{E}^* = (x_R^*, x_L^*, y_R^*, y_L^*, z_R^*, z_L^*)$ is complex and difficult to analyze mathematically, we adopt laterality frequency dynamic models, instead of population dynamics, to investigate the behavior of a system containing all three species with both types of laterality.

The variables $(x_R, x_L, y_R, y_L, z_R, z_L)$ are converted to $(p_x x, (1 - p_x)x, p_y y, (1 - p_y)y,$

$p_z z$, $(1 - p_z)z$), where p_x , p_y , and p_z are the frequency of righties of species x , y , and z , respectively; x , y , and z are the population sizes of these species. We assumed that the logarithmic fitness of righties and lefties in each of the three species, denoted by f_i and g_i , respectively, is determined by the efficiencies of cross and parallel predation, as in population Model 2, as shown in Table A1. The mean population fitness, denoted by w_i , is $p_i f_i + (1 - p_i)g_i$. Therefore, the frequency dynamics are given by:

$$dp_i / dt = p_i [f_i - w_i] = p_i (1 - p_i)(f_i - g_i). \quad (\text{A8})$$

Therefore, the frequency dynamics are written:

$$\begin{aligned} dp_x / dt &= p_x (1 - p_x) m [(C_{xy} - P_{xy})(1 - 2p_y)y + (C_{xz} - P_{xz})(1 - 2p_z)z], \\ dp_y / dt &= p_y (1 - p_y) [m(C_{yz} - P_{yz})(1 - 2p_z)z - (C_{yz} - P_{yz})(1 - 2p_x)x], \\ dp_z / dt &= p_z (1 - p_z) [-(C_{xz} - P_{xz})(1 - 2p_x)x - (C_{yz} - P_{yz})(1 - 2p_y)y]. \end{aligned} \quad (\text{A9})$$

Here, we investigate the conditions resulting in the stable coexistence of the three species. The one and only dimorphic equilibrium is $(p_x, p_y, p_z) = (1/2, 1/2, 1/2)$, which we denote by \mathbf{p}^* .

We analyze the local stability of \mathbf{p}^* under the assumption that the population size reaches equilibrium: $(x, y, z) = (2x^*, 2y^*, 2z^*)$. We express the eigenvalue equation of the Jacobian matrix taken at the dimorphic equilibrium \mathbf{p}^* of the frequency dynamics (A9) as $\lambda^3 + a_2 \lambda^2 + a_1 \lambda + a_0 = 0$, where the coefficients are:

$$a_2 = 0, \quad (\text{A10A})$$

$$a_1 = \left[x^* y^* (C_{xy} - P_{xy})^2 + x^* z^* (C_{xz} - P_{xz})^2 + y^* z^* (C_{yz} - P_{yz})^2 \right] m / 16, \quad (\text{A10B})$$

$$a_0 = (C_{xy} - P_{xy})(C_{xz} - P_{xz})(C_{yz} - P_{yz})(1 - m) m x^* y^* z^* / 64. \quad (\text{A10C})$$

At least one of the eigenvalues has a positive real part when this equilibrium is an unstable focus. The dimorphic equilibrium is locally unstable when $a_2 \leq 0$, $a_1 \leq 0$, or

$a_2 a_1 - a_0 \leq 0$. Since $a_2 = 0$, at least one of the eigenvalues has a non-negative real part and the sign of $a_2 a_1 - a_0$ is always opposite that of a_0 . Moreover, all the coefficients are always positive or zero ($C_{ij} > P_{ij}$ and $m \leq 1$); therefore, $a_2 a_1 - a_0 \leq 0$ is satisfied. If $C_{ij} < P_{ij}$ for 1 or 3 combinations, a_0 is negative, and the equilibrium is a saddle.

If $m = 1$ and $a_0 = 0$, the eigenvalues of the Jacobian matrix at \mathbf{p}^* are 0 and $\pm\sqrt{-a_1}$. Therefore, this linearized system has a neutrally stable equilibrium, and the stability property is determined by higher-order analysis. A Lyapunov function (Eq. A5) shows the global stability of this equilibrium (Online App. A).

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Online Table

Table A1. Logarithmic fitness of righties (f_i) and lefties (g_i).

Parameter	Definition
f_x	$m \left[C_{xy}y(1-p_y) + P_{xy}yp_y + C_{xz}z(1-p_z) + P_{xz}zp_z \right] - d_x$
g_x	$m \left[C_{xy}yp_y + P_{xy}y(1-p_y) + C_{xz}zp_z + P_{xz}z(1-p_z) \right] - d_x$
f_y	$m \left[C_{yz}z(1-p_z) + P_{yz}zp_z \right] - C_{xy}x(1-p_x) - P_{xy}xp_x - d_y$
g_y	$m \left[C_{yz}zp_z + P_{yz}z(1-p_z) \right] - C_{xy}xp_x - P_{xy}x(1-p_x) - d_y$
f_z	$r \left(1 - \frac{z}{K} \right) - C_{xz}x(1-p_x) - P_{xz}xp_x - C_{yz}y(1-p_y) - P_{yz}yp_y$
g_z	$r \left(1 - \frac{z}{K} \right) - C_{xz}xp_x - P_{xz}x(1-p_x) - C_{yz}yp_y - P_{yz}y(1-p_y)$

Role of omnivory for fluctuation of lateral dimorphism in fishes

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Introduction

Two morphological types, lefty and righty, have been found in several fish species. A lefty fish has its mouth opening to the right, causing the left side of its head to face the front, while a righty has its mouth to the left, causing the right side of the head to face forward¹⁻⁶. This lateral dimorphism is a typical example of “antisymmetry”⁷. Lateral antisymmetry in fishes has genetic bases and bimodal distribution of signed differences⁸. It differs from fluctuating asymmetry which distributes normally and caused by stochastic events in developmental stages.

Several features of the lateral dimorphism have been described: first, the laterality is inheritable in a Mendelian 1-locus-2-allele fashion with lefties dominating^{2,5}; second, the proportion of lefties in the cichlid population over 11 years showed a periodical oscillation around 0.5²; and third, laterality appears in both prey and predator fish species, and predators usually attack prey of the opposite morphological type³. Nakajima et al.⁹ called “cross predation” as predation when predators exploit prey of the opposite laterality, that is, lefties and righties of the same predator species respectively feed on righties and lefties of the prey species. Nakajima et al.⁹ also defined “parallel predation” as a situation in which predators feed on prey of the same laterality. Cross predation would lead to the transition of survival and reproductive advantages between the two types: when lefty dominates in a predator species, righty prey would decrease; then, lefties would become dominant in a prey species, followed by domination of righties in a predator species⁹. Nakajima et al.⁹ investigated this hypothesis, introducing a mathematical model of a simple 1-prey-1-predator system and three trophic level systems with and without omnivory.

Model 1: 1-Predator-1-Prey System

This food web includes a predator species x , and prey species z . Nakajima et al.⁹ assumed that fish reproduce asexually and that laterality is inheritable. We denote the population sizes of lefties and righties of species y and z by y_L and y_R , and z_L and z_R , respectively. Since laterality is considered antisymmetric, the rates of growth, predation, and death must be symmetric between lefties and righties. The dynamics of two species were described with linear functional response:

$$\frac{dy_R}{dt} = \left[m(C_{yz}z_L + P_{yz}z_R) - d_y \right] y_R, \quad \frac{dy_L}{dt} = \left[m(C_{yz}z_R + P_{yz}z_L) - d_y \right] y_L, \quad (1A,B)$$

$$\frac{dz_R}{dt} = \left[r \left(1 - \frac{z_R + z_L}{K} \right) - C_{yz} y_L - P_{yz} y_R \right] z_R, \quad \frac{dz_L}{dt} = \left[r \left(1 - \frac{z_R + z_L}{K} \right) - C_{yz} y_R - P_{yz} y_L \right] z_L, \quad (1C,D)$$

where $C_{ij} (\geq 0)$ and $P_{ij} (\geq 0)$ are the efficiencies of predation when predator i preys on prey j with the opposite (i.e., cross predation) or the same (i.e., parallel predation) laterality, respectively; $m (\leq 1)$ is the metabolic rate; $d_y (\leq 1)$ is the death rate of the predator; and $r (> 0)$ and $K (> 0)$ are the intrinsic rate of population increase and the carrying capacity of the prey species, respectively. This system has an equilibrium $(y_L, y_R, z_L, z_R) = (y^\dagger, y^\dagger, z^\dagger, z^\dagger)$, at which all four populations coexist. Nakajima et al.⁹ confirmed the global stability of this 2-species system at this equilibrium using a Lyapunov function. The linearized system surrounding the equilibrium has a neutrally stable equilibrium. The computer simulations using Euler method showed periodic oscillations of laterality frequencies in both prey and predator. Nakajima et al.⁹ also investigated the effects of demographic stochasticity using computer simulations. The oscillations of laterality frequencies were nearly periodic, that were similar to field observations^{2,3}

Model 2: Three-Trophic-Level System

Next, Nakajima et al.⁹ added a top predator species x , which consumes species y , to the former y - z food web. We describe righties and lefties of x as x_R and x_L , respectively. As one would expect, the influence of cross predation is similar to the former model Eq. 1: when x_R dominates in species x , y_L would decrease and hence y_R would dominate automatically, followed by the decrease of its prey, z_L . The Lyapunov function showed that this system is globally stable.

The story is more complicated when the top predator x also preys on the bottom prey z , because this “omnivory” of species x imposes contradictory selective pressures on the bottom trophic level (Fig. 1). In this food web, when lefties dominate in bottom prey species, righty consumers have an advantage, which in turn conveys an advantage to lefty top predators. If we consider predation on the bottom prey by the top predator (shown by the dashed arrows in Fig. 1), however, righties dominate among the top predator when lefties dominate among the bottom prey. Although it is possible to think that the fitness of both righties and lefties is equal in the top predator, observations of oscillating frequencies of righties suggest that advantages are alternately conferred between the two phenotypes^{1,2}. To investigate how this transition in advantages among the top predators occurs in the wild, Nakajima et al.⁹ investigated a mathematical model that has an additional omnivory term.

Each frequency dynamics of six populations is similar to

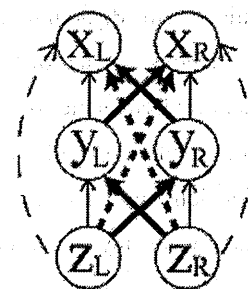


Fig. 1. Arrows indicate the directions of food intake; thick arrows: cross predation; thin arrows: parallel predation. When the top predator is omnivorous, dashed arrows indicate intake from z to x .

Eq. 1, with additional predation terms including several new parameters (C_{xz} , P_{xz} , C_{xy} , and P_{xy}), and equations related to the top predator. We should also mention that the system loses omnivory when $C_{xz} = P_{xz} = 0$. We describe x_R, x_L, y_R, y_L, z_R and z_L as a vector $\mathbf{E} = (x_R, x_L, y_R, y_L, z_R, z_L)$. There are four equilibria that consist of equal populations of both types in each species: first, the top and intermediate predators become extinct, denoted by $\mathbf{E}^s = (0, 0, 0, 0, z_R^s, K - z_R^s)$; second, the top predator becomes extinct, $\mathbf{E}^\dagger = (0, 0, y^\dagger, y^\dagger, z^\dagger, z^\dagger)$; third, the intermediate predator becomes extinct, $\mathbf{E}^\ddagger = (x^\ddagger, x^\ddagger, 0, 0, z^\ddagger, z^\ddagger)$; and fourth, the three species coexist, $\mathbf{E}^* = (x^*, x^*, y^*, y^*, z^*, z^*)$; where $y^\dagger, z^\dagger, x^\ddagger, z^\ddagger, x^*, y^*$, and z^* are given by equations in Nakajima et al.⁹. Note that equilibrium \mathbf{E}^\dagger is equal to the equilibrium of Eq. 1.

The population size of righty and lefty in a species differs in 28 other equilibria in Model 2. These and one trivial equilibrium $(0, 0, 0, 0, 0, 0)$ are invadable by other species or types of species, thus the system converges on the symmetric equilibrium, *i.e.*, $\mathbf{E}^s, \mathbf{E}^\ddagger, \mathbf{E}^\dagger$ or \mathbf{E}^* . Although an asymmetric equilibrium $\mathbf{E}^\# = (0, x^\#, y^\#, 0, z_1^\#, z_2^\#)$, where $x^\#, y^\#, z_1^\#$ and $z_2^\#$ are given by Nakajima et al.⁹, includes lefties and righties in both predators and prey, it is not maintained, but moves to another state and finishes at symmetric equilibrium. Nakajima et al.⁹ investigated two aspects of the stability of this asymmetric equilibrium $\mathbf{E}^\#$: First, whether the absent type in species x or y invades equilibrium $\mathbf{E}^\#, i.e.$, whether $(dx_R / dt) / x_R > 0$ or $(dy_L / dt) / y_L > 0$ are satisfied at $\mathbf{E}^\#$; and second, whether this equilibrium is locally stable for any perturbation of existing populations, x_L, y_R, z_R and z_L . In the numerical analysis, either one of the invadability inequalities is satisfied whenever $\mathbf{E}^\#$ is locally stable, if the efficiency of cross predation exceeds that of parallel predation ($C_{ij} > P_{ij}$).

Nakajima et al.⁹ examined the dynamic behavior of six populations using computer simulations. With many parameter sets of various values of predation efficiencies, the frequencies of laterality in each population fluctuated significantly; they converged on periodic oscillations in a manner similar to field data^{2,3}, as long as no species became extinct. The computer simulations well described the coexistence of lefties and righties in all three species on a limit cycle. If omnivory exists, the dynamics of three species is unstable when the total population sizes of each species are constant. Simulations with demographic stochasticity showed a not perfect but nearly periodic oscillations. The oscillations of each of the three species had the same period, but they were not synchronized. The laterality frequencies of predators were always followed by those of their prey.

The simulation result differed when the assumption $C_{ij} > P_{ij}$ was not satisfied. When parallel predation dominates in all predators, *i.e.*, $C_{ij} < P_{ij}$, the laterality frequencies did not oscillate around \mathbf{E}^* permanently for any of the parameter values we investigated; it changed to various monomorphic states or 2-species systems (equilibrium \mathbf{E}^\dagger or \mathbf{E}^\ddagger).

Discussion

In the symposium, we obtained several valuable comments. First comment was about the global stability: the audience expected that a Lyapunov function of the 3-species system (Model 2)

must be found as in 1-predator-1-prey system. Actually, Nakajima et al.⁹ found a Lyapunov function of 2-species (Model 1) and 3-species system without omnivory (Model 2 with $C_{xz} = P_{xz} = 0$) and showed its global stability, with an assumption of the metabolic rates of predators $m = 1$. Under the same assumption ($m = 1$), we also found a Lyapunov function L of 3-species system with omnivory:

$$L = x^*[x_R/x^* - 1 - \log(x_R/y^*)] + x^*[x_L/x^* - 1 - \log(x_L/x^*)] + y^*[y_R/y^* - 1 - \log(y_R/y^*)] + y^*[y_L/y^* - 1 - \log(y_L/y^*)] + z^*[z_L/z^* - 1 - \log(z_L/z^*)] + z^*[z_R/z^* - 1 - \log(z_R/z^*)],$$

$$\frac{dL}{dt} = \frac{[(C_{yz} + P_{yz})d_x K - (C_{xz} + P_{xz})d_y K + (C_{xy} + P_{xy})(z_R + z_L - K)r]^2}{(C_{xy} + P_{xy})^2 Kr},$$

where the asterisk indicates the equilibrium E^* , $d_x (\leq 1)$ is the death rate of the top predator. The function L satisfies $L \geq 0$ and $dL/dt \leq 0$, each of the equalities holds at the equilibrium. Although, we hardly think the assumption $m = 1$ is general because of the omnivorous top predator. Therefore, Nakajima et al.⁹ did not show the function L but investigated the global stability numerically with computer simulations.

Second comment was about the effects of demographic stochasticity on population invadability. As shown above, Nakajima et al.⁹ showed the transitions of equilibria to the symmetric systems caused by invasions. However, it is not clear whether the monomorphic state (e.g., all individuals are lefty) is always unstable for some species in more complex food webs, especially when we consider demographic stochasticity.

Finally we would like to thank the attendance giving us other valuable suggestions.

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1 **A Population Genetic Model for Lateral Dimorphism Frequency in Fishes**

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1 **Abstract**

2 Two morphological types, righty and lefty, are found in several fish species. Righty
3 predators mainly prey on lefty prey and vice versa (called “cross predation”). This
4 dimorphism is heritable in a Mendelian one-locus-two-allele fashion. The frequency of
5 righty individuals in a population oscillates periodically. To determine the effect of cross
6 predation on this oscillation, we constructed mathematical models that describe a genetic
7 basis of lateral dimorphism assuming genetic drift in a one-predator-two-prey system and
8 three trophic levels with omnivory. Both models have an equilibrium of both righty and
9 lefty types at a frequency of 0.5. Mathematical analyses and computer simulations
10 showed that the dimorphism is maintained and that its frequency oscillated with or
11 without genetic drift. Large degrees of drift and high intrinsic growth rates and predation
12 efficiencies of prey species caused the period of frequency oscillation to be short and
13 amplified. When cross predation decreased as a proportion of all predation, the righty
14 frequency of a prey species fluctuated non-periodically. These differences in fluctuation
15 patterns were observed in natural systems. Our model suggests that both cross predation
16 and genetic drift dictate the maintenance of dimorphism and the patterns of its
17 fluctuations.

18
19 Key words:

20 Laterality, gene frequency dynamics, antisymmetry, prey-predator system, dimorphism,
21 frequency-dependent selection

Introduction

Two morphological types, righty and lefty, are found in several fish species (Hori 1991, 1993, 2000; Liem and Stewart 1976; Mboko et al. 1998; Seki et al. 2000). In a righty individual, the right side of its head face front and thus its mouth opens leftward, due to right joint of mandible to suspensorium taking a position frontward, ventrally, and outside compared to its left joint. In a lefty individual, the left side has these characteristics. This dimorphism, called laterality, is a typical example of “antisymmetry” (Van Valen 1962), which has a bimodally distributed, asymmetric character frequency. Every individual is classified as righty or lefty (Hori 1991, 1993, 2000; Mboko et al. 1998; Seki et al. 2000). Although the shape of the distribution curve did not change significantly over 10 years in one fish population, the frequency of righty individuals was unstable, oscillating around 0.5 (Hori 1993, 2000). Interestingly, several investigations have suggested that this lateral dimorphism is heritable in a Mendelian one-locus-two-allele fashion with lefty dominating over righty (Hori 1993, 2000; Mboko et al. 1998; Seki et al. 2000).

Nakajima et al. (2004) suggested a possible maintenance mechanism. They focused on biased predation related to lateral dimorphism: righty predators mainly prey on lefty prey and vice versa (Hori 2000). Such “cross predation” is in contrast to predation between the same morphological types, called “parallel predation.” Their numerical investigations of population-dynamic models indicated that the transition of survival and reproductive advantages between the two types occurs because of cross predation. Domination by lefties in predator species would be followed by a decrease of its righty prey; then automatically, lefties would become the dominant prey and righty predators would increase. Thus, the frequency of lateral dimorphism fluctuates. However,

1 mathematical analysis showed that the fluctuations eventually converge to a stable
 2 equilibrium in a one-predator-one-prey model (Nakajima et al. 2004).

3 We considered stochasticity as one factor causing the fluctuation. We investigated
 4 the difference between stochastic and non-stochastic dynamics. Because the population
 5 size and community structure of cichlids at the study site in Lake Tanganyika seem to be
 6 stable (Hori 1997), we considered a genetic basis of lateral dimorphism to introduce
 7 genetic drift into a model with constant population sizes.

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A one-predator-two-prey system

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Consider a one-predator-two-prey food web, as is frequently observed at the
 research sites of lateral dimorphism, such as Lake Tanganyika (Hori 1987; Hori et al.
 1993). We denote the population sizes of predator species x and prey species y and z as x ,
 y , and z , respectively. We followed the expressions of the population dynamics of x , y ,
 and z described in Hutson and Vickers (1983):

15

$$dx/dt = [m(A_{xy}y + A_{xz}z) - d_x - ex]x, \quad (1A)$$

16

$$dy/dt = \left[r_y \left(1 - \frac{y + \alpha_1 z}{k_y} \right) - A_{xy}x \right] y, \quad (1B)$$

17

$$dz/dt = \left[r_z \left(1 - \frac{z + \alpha_2 y}{k_z} \right) - A_{xz}x \right] z, \quad (1C)$$

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19

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21

22

where $A_{ij} (> 0)$ is the efficiency of predation when predator i preys on prey j ; $m (\leq 1)$ is the
 metabolic rate; $d_x (\leq 1)$ and e are the death rate and the density effect of the predator,
 respectively; $r_i (> 0)$ and $k_i (> 0)$ are the intrinsic rate of population increase and the
 carrying capacity of the prey species i , respectively; and α_i is the competitive effect of
 species i on another species in the same trophic level. Equation 1 has the equilibrium

1 $\bar{\mathbf{E}} = (\bar{x}, \bar{y}, \bar{z})$. Details of the equilibrium and the parameter conditions that allow these
 2 species to coexist permanently are shown in App. A and in Hutson and Vickers (1983).

3 We considered a one-locus-two-alleles genetic model of laterality for each of the
 4 three species, assuming the persistence of a three-species system (Eq. 1). This simple
 5 assumption of inheritance facilitates the analysis. The assumption is also reasonable:
 6 lefty is the dominant allele and righty the recessive allele in several fish species. This
 7 situation has been observed in *Perissodus* spp. (Hori 1993, 2000; Takahashi and Hori
 8 1998) and other fish species (Hori unpublished; Seki et al. 2000). When we let L and l be
 9 the alleles for lefty and righty, respectively, the genotype of a lefty individual is LL or Ll ;
 10 that of a righty is ll . We denote the gene frequency of allele l in species i as p_i . The
 11 phenotypic frequencies of LL , Ll , and ll are $(1 - p_i)^2$, $2p_i(1 - p_i)$, and p_i^2 , respectively. We
 12 assumed that the logarithmic fitness of righties and lefties in each of the three species,
 13 denoted by f_i and g_i , respectively, is determined by the efficiencies of cross predation and
 14 parallel predation shown in Table 1. In Nakajima et al. (2004), we defined C_{ij} and P_{ij} as
 15 the cross-predation and parallel-predation efficiencies of predator i on prey j , respectively.
 16 Note that $A_{ij} = C_{ij} + P_{ij}$ and $K_i = k_i/2$. We assumed that the competitive effect α_i , carrying
 17 capacity K_i , and density effect e are the same between lefty and righty individuals. These
 18 assumptions are simple but may be appropriate for describing the basic antisymmetry in
 19 predation. The marginal fitnesses (Smith 1998) of alleles L and l of species i , denoted by
 20 $w_{L,i}$ and $w_{l,i}$, are:

$$21 \quad w_{L,i} = p_i g_i + (1 - p_i) f_i \quad (2A)$$

22 and

$$23 \quad w_{l,i} = p_i f_i + (1 - p_i) g_i. \quad (2B)$$

1 The mean population fitness, denoted by w_i , is $p_i w_{L,i} + (1 - p_i) w_{R,i}$. Therefore, the gene
 2 frequency dynamics are given by:

$$3 \quad dp_i / dt = p_i [w_{L,i} - w_i] = p_i (1 - p_i) (w_{L,i} - w_{R,i}). \quad (3)$$

4 From Eq. 3, we obtain a model for the gene frequency dynamics of the three species:

$$5 \quad dp_x / dt = (1 - p_x) p_x^2 m [(C_{xy} - P_{xy})(1 - 2p_y^2)y + (C_{xz} - P_{xz})(1 - 2p_z^2)z],$$

$$6 \quad dp_y / dt = (C_{yz} - P_{yz})(2p_x^2 - 1)z(1 - p_y)p_y^2 x, \quad (4)$$

7 and

$$8 \quad dp_z / dt = (C_{xz} - P_{xz})(2p_x^2 - 1)(1 - p_z)p_z^2 x.$$

9 The one and only dimorphic equilibrium is $(p_x, p_y, p_z) = (\sqrt{1/2}, \sqrt{1/2}, \sqrt{1/2})$, which
 10 we denote by \mathbf{p}^* . From the Hardy-Weinberg law, the numbers of lefties and righties are
 11 the same (the phenotype frequencies are both 1/2) at this equilibrium.

12 We linearized and investigated the local stability of gene frequency dynamics (Eq.
 13 4), under which the populations of the three species (including both righties and lefties)
 14 converged on the coexisting equilibrium $\bar{\mathbf{E}}$. The linear approximation suggests that \mathbf{p}^* is
 15 neutrally stable, regardless of the parameter values (App. A).

16 We examined the global behavior of the simultaneous dynamics of gene frequency
 17 (Eq. 4) using computer simulations with the Runge-Kutta method of order 4 and many
 18 parameter sets with various predation efficiency values. The total population size of each
 19 species (x , y , and z) was given as a constant with a value set at equilibrium $\bar{\mathbf{E}}$. In all cases,
 20 the gene frequencies converged on periodic oscillations for a long time period (Figs. 1A
 21 and 1B; correlogram: 1C). The laterality frequencies were not synchronized among the
 22 trophic levels; those of predators were always followed by those of their prey (e.g., righty
 23 x was followed by lefty z [= 1 - (righty z)] and lefty y [= 1 - (righty y)]). Laterality

Fig. 1
 HERE

1 frequencies oscillated around 0.5 with some value combinations of the initial laterality
 2 frequencies of simulations and predation efficiencies (Fig. 1A). At some values of initial
 3 laterality frequencies, the averages of laterality frequencies in prey species were biased
 4 towards 0 or 1 (Fig. 1B), although the laterality frequency of total prey ($= [p_y^2 y + p_z^2 z] / [y$
 5 $+ z]$) oscillated around 0.5 in most cases. These time-series analyses showed that periods
 6 were the same among three species and were longer when the intrinsic growth rate was
 7 lower (e.g., Fig. 1A vs. Fig. 1B) or the predation efficiency was greater (not shown).

8 Next, we added the effect of genetic drift (Roughgarden 1979):

$$9 \quad dp_i / dt = p_i (1 - p_i) (w_{i,i} - w_{L,i}) + \sigma_i \zeta_i p_i (1 - p_i), \quad (5)$$

10 where ζ_i denotes white noise and σ_i is the magnitude of genetic drift of species i , which
 11 depends on the absolute population size and the generation length (Hakoyama and Iwasa
 12 2000). We investigated numerically how the range of $\sigma_i \zeta_i$ values affects the laterality
 13 frequency by using spectrum analysis for computer simulations with the 4th-order
 14 Runge-Kutta method. Parameter ζ_i took uniformly random variables between -1 and 1 .
 15 Simulation results varied with time-step width. If time step Δt is 0.001 , $\zeta_i(t)$ does not
 16 change within each time step Δt , although $\zeta_i(t)$ does not change throughout 0.002 if time
 17 step Δt is $0.002\Delta t$. The magnitude of the noise effect is proportional to the square root of
 18 the time step. Therefore we kept $\sigma_i / \sqrt{\Delta t}$ constant when we used a different time step Δt .

19 The results showed that stochasticity within some level did not interfere with the cyclic
 20 fluctuation caused by cross predation (simulation results: Figs. 2A-2D; correlogram: 2E).

Fig. 2
 HERE

21 In addition, σ_i and the amplitude of cyclic fluctuations became larger, and the periods
 22 became longer (see Fig. 2A vs. Fig. 2C for simulation results). Also, in prey species with
 23 small P_{ij}/C_{ij} , non-periodic fluctuation caused by genetic drift appeared; the center of the
 24 cyclic fluctuation was unsettled, although the cyclic period did not change significantly

1 (e.g., species z in Fig. 2B vs. Fig. 2A). This fluctuation of periodic oscillation
2 disappeared when genetic drift was small in species with small P_{ij}/C_{ij} compared with the
3 other prey species (e.g., species z in Fig. 2D). Instability increased when σ_i was too large
4 and the duration for which laterality frequency was near 0 or 1 increased (not shown).

5

6 **A three-trophic-level system with omnivory**

7 The gene-frequency model (Eq. 3) can also be applied to another food web
8 introduced in Nakajima et al. (2004): a web composed of an omnivorous predator species
9 x , an intermediate prey y , and a bottom prey z . Here, “omnivory” is defined as the
10 feeding on nonadjacent trophic levels (Pimm and Lawton 1978; Pimm 1982). Species x
11 preys on species y and z ; species y also preys on species z . Nakajima et al. (2004)
12 investigated the stability of this food web because the top predator x receives
13 contradictory selective pressures from the bottom prey z . When lefty dominates in z ,
14 righty in x and y increase. However, because righty y increases, then also lefty in x must
15 increase. Laterality frequencies in all species fluctuated, as observed in the field (Hori
16 1993, 2000). Therefore, the opposite selective pressure on the omnivorous predator
17 might be balanced and might disappear.

18 We confirmed this result with a gene-frequency dynamics model. The dynamics of
19 the population sizes x , y , and z were described with the Lotka-Volterra type functional
20 response as Eq. 3. The details of dynamics and its equilibrium $\mathbf{E}^* = (x^*, y^*, z^*)$ are
21 shown in Holt and Polis (1997) and App. B. In our model, we assumed that these three
22 species permanently coexist; we verified this assumption in a three-species population
23 dynamics model (see App. B). We then considered the dynamics of the gene frequencies
24 of two alleles on one locus (Eq. 3). The fitness functions of species x are exactly the same

Table 2
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1 as those given in Table 1; they are slightly different in species y and z, as shown in Table

2. The gene-frequency dynamics are then:

$$3 \quad dp_x / dt = (1 - p_x) p_x^2 m \left[(C_{xy} - P_{xy})(1 - 2p_y^2) y + (C_{xz} - P_{xz})(1 - 2p_z^2) z \right], \quad (6A)$$

$$4 \quad dp_y / dt = (1 - p_y) p_y^2 \left[m(C_{yz} - P_{yz})(1 - 2p_y^2) z - (C_{xy} - P_{xy})(1 - 2p_x^2) x \right], \quad (6B)$$

5 and

$$6 \quad dp_z / dt = (1 - p_z) p_z^2 \left[-(C_{xz} - P_{xz})(1 - 2p_x^2) x - (C_{yz} - P_{yz})(1 - 2p_y^2) y \right]. \quad (6C)$$

7 The one and only dimorphic equilibrium is again \mathbf{p}^* . We investigated the local
8 stability of the gene-frequency dynamics (Eq. 6) under which the populations of three
9 species (including both righties and lefties) are at the coexisting equilibrium \mathbf{E}^* . Local
10 stability analysis showed \mathbf{p}^* to be an unstable focus regardless of the parameter values
11 (App. A). Note that when $C_{xz} = P_{xz} = 0$ (no omnivory) or when $m = 1$ (no energetic loss by
12 predation), the linear approximation suggests that \mathbf{p}^* is neutrally stable.

13 We examined the global behavior of the simultaneous dynamics of the gene
14 frequency (Eq. 6) using computer simulations, again with various values of predation
15 efficiencies and constant total population sizes set at \mathbf{E}^* , with and without genetic drift.
16 Computer simulations showed oscillations (Fig. 3A) like those in the
17 one-predator-two-prey system. The simulations described well the coexistence of lefties
18 and righties in all three species on a limit cycle. The average laterality frequencies in all
19 three species were about 0.5. However, this difference disappeared when we introduced
20 genetic drift and P_{ij}/C_{ij} was relatively large. The laterality frequency of the top predator x
21 fluctuated within a smaller range and was biased toward a monomorphic state (Fig. 3B).
22 The center of the fluctuation in species x approached 0.5 when drift in the bottom prey z
23 was reduced (Fig. 3C). The other effect of σ_i was similar to that in the

Fig. 3
HERE

1 one-predator-two-prey model (Eq. 5): when σ_i increased, so did the amplitude of the
2 laterality frequency fluctuation and the fluctuation period.

3 As in the numerical analysis of population dynamics of Nakajima et al. (2004), the
4 local stability of \mathbf{p}^* depends on whether the assumption of $C_{ij} > P_{ij}$ is satisfied. When
5 parallel predation dominates in all predators (i.e., $C_{ij} < P_{ij}$), \mathbf{p}^* is a saddle point. This
6 result suggests that the laterality frequencies do not oscillate permanently around \mathbf{p}^* . In
7 simulations in which $C_{ij} < P_{ij}$, some species become monomorphic or extinct.

8 9 Discussion

10 Our mathematical investigations and numerical simulations agreed well, especially
11 for the three-trophic-level food web, with those of Nakajima et al. (2004) who
12 investigated the population dynamics of lefties and righties without consideration of
13 genetic bases. Our computer simulations showed that some genetic drift does not
14 interfere with the maintenance of lateral dimorphism and its frequency oscillation.
15 Generally, genetic drift in a very small population reduces genetic diversity (Begon et al.
16 1996). Our simulations supported this theory: gene frequency approached 0 or 1 for a
17 long time when the range of drift was relatively wide in relation to the population sizes.
18 Prey species with heavier predation or smaller intrinsic growth rates or both had larger
19 oscillation amplitudes than did other species, even without genetic drift (e.g., species y in
20 Fig. 1B). Such a combination of parameters makes the population size smaller than that
21 of the other prey species. When the differences of A_{ij} and r_i are larger between the prey
22 species, the difference in prey population sizes are larger ($\bar{y} < \bar{z}$ when $r_y < r_z$ and/or $A_{xy} >$
23 A_{xz} ; see the equations of population sizes [Eq. A1]). Therefore, genetic drift may amplify
24 the intrinsic oscillation in the smaller population. Previous studies of laterality gene

1 frequency with time delays in one trophic level showed that when reproductive success is
2 weakly dependent on phenotypic frequency, dimorphism will be lost owing to genetic
3 drift (Takahashi and Hori 1994, 1998). In our model, cross predation may play the same
4 role as frequency dependent selection. Cross predation itself maintains dimorphism in
5 both prey and predator and also might protect dimorphism from genetic drift.

6 We observed a non-periodic fluctuation of laterality frequency in our simulations
7 only when the three populations experienced genetic drift. This unstable fluctuation was
8 distinguished by relatively large P_{ij}/C_{ij} . For example, the frequency of species z
9 fluctuated periodically when $P_{xy}/C_{xy} = P_{xz}/C_{xz} = 0.06$ (Fig. 2A), but it did not when P_{xy}/C_{xy}
10 $= 0.06$ and $P_{xz}/C_{xz} = 0.66$ (Fig. 2B and 2C; note that we assumed $P_{ij}/C_{ij} < 1$). The rapid
11 alternation of major laterality in predator species x amplifies the oscillation of laterality
12 frequency in prey y, although its center remains near 0.5. This fluctuation was found in
13 predator species x in the three-trophic level system with omnivory (Fig. 3B). Although
14 the same fluctuation was observed when the total predation efficiencies differed among
15 prey species (i.e., A_{xz}/A_{xy} was small), the magnitude of instability was smaller.

16 These effects were found when genetic drift was present. Our simulations also
17 revealed that the behaviors of lateral dimorphism frequencies in each species depended
18 on the biological parameters of the species, irrespective of the presence of genetic drift.
19 The magnitude of the intrinsic growth rates in prey species influenced the periods of
20 morphological frequency fluctuations. When the growth rate was relatively high, the
21 period was short. This result can be explained by the main morphological type of prey
22 rapidly recovering its population size to become the dominant type. The periods were
23 also short when the predation efficiencies were large because of the rapid decrease of the
24 main prey type. Especially in a food web with three trophic levels, the parameter values

1 of the bottom prey species z affected the behavior of the whole system more than the
 2 middle prey species y did.

3 The minority advantage of lateral dimorphism is not limited to one species but is
 4 seen among species. It therefore differs from sexual selection, in which any advantage
 5 must be intraspecific. We must emphasize this difference because the most frequently
 6 cited example of antisymmetry, claw size in male fiddler crabs, might be maintained by
 7 sexual selection (Pope 2000; Pratt and Mclain 2002). The crab claw is a male
 8 characteristic, but lateral antisymmetry in fishes is independent of sex. This sex
 9 independence has been observed in *Perissodus* spp. (Hori 1991; Takahashi and Hori
 10 1998), *T. temporalis* (Mboko et al. 1998), *R. flumineus* (Seki et al. 2000), and other
 11 species (Hori unpublished). The lateral antisymmetry of fishes may constitute a more
 12 common and more typical example of antisymmetry.

14 Appendix

15 Appendix A: Stability of Gene Frequency Dynamics

16 Model 1 (Eq. 1) has an interior equilibrium $\bar{\mathbf{E}}$:

$$17 \quad \bar{x} = r_y r_z d_x (\alpha_1 \alpha_2 - 1) + r_y r_z m [A_{xy} (K_y - \alpha_1 K_z) + A_{xz} (K_z - \alpha_2 K_y)] / D, \quad (A1A)$$

$$18 \quad \bar{y} = A_{xz} K_z r_y m (A_{xz} K_y m - \alpha_1 d_x) + A_{xy} K_y r_z m (d_{xz} - A_{xz} K_z m) + d_x r_y r_z (K_y - \alpha_2 K_z) / D, \quad (A1B)$$

$$19 \quad \bar{z} = A_{xz} K_z r_y m (d_x - A_{xy} K_y m) + A_{xy} K_y r_z m (A_{xy} K_z m - \alpha_2 d_x) + d_x r_y r_z (K_z - \alpha_1 K_y) / D, \quad (A1C)$$

$$20 \quad \text{where } D = m [A_{xz} K_z r_y (A_{xz} - \alpha_1 A_{xy}) + A_{xy} K_y r_z (A_{xy} - \alpha_2 A_{xz})] + d_x r_y r_z (1 - \alpha_1 \alpha_2)$$

21 We linearized the gene frequency dynamics (Eq. 4) and obtained the eigenvalues of
 22 the Jacobian matrix taken at the dimorphic equilibrium \mathbf{p}^* and the coexistent
 23 equilibrium $\bar{\mathbf{E}}$:

$$0, \pm \sqrt{(2\sqrt{2}-3)m\bar{x}\left[\bar{y}(C_{xy}-P_{xy})^2 + \bar{z}(C_{xz}-P_{xz})^2\right]}. \quad (\text{A2A, B})$$

This expression indicates that \mathbf{p}^* is neutrally stable. Note that this result does not change even when $C_{ij} < P_{ij}$.

Next, we expressed the eigenvalue equation of the Jacobian matrix taken at the dimorphic equilibrium \mathbf{p}^* of the gene frequency dynamics (Eq. 5) as $\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0 = 0$, where the coefficients are:

$$a_2 = 0, \quad (\text{A3A})$$

$$a_1 = (3 - 2\sqrt{2})m\left[(C_{xy} - P_{xy})^2 x^* y^* + (C_{xz} - P_{xz})^2 x^* z^* + (C_{yz} - P_{yz})^2 y^* z^*\right], \text{ and} \quad (\text{A3B})$$

$$a_0 = \left[(10 - 7\sqrt{2})(C_{xy} - P_{xy})(C_{xz} - P_{xz})(C_{yz} - P_{yz})x^* y^* z^* m(1 - m)\right] / \sqrt{2}. \quad (\text{A3C})$$

At least one eigenvalue has a positive real part when this equilibrium is an unstable focus. The dimorphic equilibrium is locally unstable when $a_2 \leq 0$, $a_1 \leq 0$, or $a_2 a_1 - a_0 \leq 0$. Because $a_2 = 0$, at least one eigenvalue has a non-negative real part, and the sign of $a_2 a_1 - a_0$ is always opposite that of a_0 . If $a_0 < 0$, the equilibrium is a saddle point. If $a_0 > 0$, it is an unstable focus because $a_2 a_1 - a_0 \leq 0$ and $a_2 = 0$. All coefficients are always positive or zero if $C_{ij} > P_{ij}$ and $m \leq 1$.

If $C_{xz} = P_{xz} = 0$ (no omnivory) or if $m = 1$ (no energetic loss of predation), then $a_0 = 0$, so one of the three eigenvalues is zero and the other two are purely imaginary numbers. This case indicates that \mathbf{p}^* is neutrally stable in the linearized system. If $C_{ij} < P_{ij}$ for any one pair or all three pairs of species (x-y, x-z, and y-z), then $a_1 > 0$ and $a_2 a_1 - a_0 \geq 0$; thus \mathbf{p}^* is a saddle point.

Appendix B:

1 Conditions for Equilibrium Existence and the Permanence of Holt & Polis' (1997)

2 System

3 The dynamics of the three species were described with the Lotka-Volterra type
4 functional response in Holt and Polis (1997) as:

5
$$\frac{dx}{dt} = \left[m(A_{xy}y + A_{xz}z) - d_x \right] x, \quad (\text{A4A})$$

6
$$\frac{dy}{dt} = \left[mA_{yz}z - A_{xy}x - d_y \right] y, \quad (\text{A4B})$$

7
$$\frac{dz}{dt} = \left[r \left(1 - \frac{z}{k} \right) - A_{xz}x - A_{yz}y \right] z. \quad (\text{A4C})$$

8 We say that Eq. A4 is permanent when there exists a positive constant δ such that

9
$$\delta < \liminf_{t \rightarrow +\infty} (x(t), y(t), z(t))$$

10 As shown in Hofbauer and Sigmund (1998), this Lotka-Volterra type system is permanent
11 when there is a vector $\mathbf{s} = (s_1, s_2, s_3)$ that satisfies the following inequality at all boundary
12 equilibria:

13
$$s_1 \left(\frac{dx}{dt} / x \right) + s_2 \left(\frac{dy}{dt} / y \right) + s_3 \left(\frac{dz}{dt} / z \right) > 0. \quad (\text{A5})$$

14 Note that the logarithmic fitnesses in this system (i.e., those inside the parentheses in Eq.
15 A5) are linear functions of population size. We know that this inequality holds at every
16 equilibrium except for the interior equilibrium \mathbf{E}^* when all the population sizes in \mathbf{E}^* are
17 positive.

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Tables

1
2 Table 1. Logarithmic fitnesses of lefties (f_i) and righties (g_i) in the one-predator-two-prey
3 model.

f_x	$m \left[C_{xy}y(1-p_y^2) + P_{xy}yp_y^2 + C_{xz}z(1-p_z^2) + P_{xz}zp_z^2 \right] - d_x - ex$
g_x	$m \left[C_{xy}yp_y^2 + P_{xy}y(1-p_y^2) + C_{xz}zp_z^2 + P_{xz}z(1-p_z^2) \right] - d_x - ex$
f_y	$r_y \left(1 - \frac{y + \alpha_1 z}{K_y} \right) - C_{xy}x(1-p_x^2) - P_{xy}xp_x^2$
g_y	$r_y \left(1 - \frac{y + \alpha_1 z}{K_y} \right) - C_{xy}xp_x^2 - P_{xy}x(1-p_x^2)$
f_z	$r_z \left(1 - \frac{z + \alpha_2 y}{K_z} \right) - C_{xz}x(1-p_x^2) - P_{xz}xp_x^2$
g_z	$r_z \left(1 - \frac{z + \alpha_2 y}{K_z} \right) - C_{xz}xp_x^2 - P_{xz}x(1-p_x^2)$

- 1 Table 2. Logarithmic fitnesses of lefties (f_i) and righties (g_i) in prey species in a
- 2 three-trophic-level food web with omnivory.

$$f_y = m \left[C_{yz}z(1-p_z^2) + P_{yz}zp_z^2 \right] - C_{xy}x(1-p_x^2) - P_{xy}xp_x^2 - d_y$$

$$g_y = m \left[C_{yz}zp_z^2 + P_{yz}z(1-p_z^2) \right] - C_{xy}xp_x^2 - P_{xy}x(1-p_x^2) - d_y$$

$$f_z = r_z(1-z/K_z) - C_{yz}y(1-p_y^2) - P_{yz}yp_y^2 - C_{xy}x(1-p_x^2) - P_{xy}xp_x^2$$

$$g_z = r_z(1-z/K_z) - C_{yz}yp_y^2 - P_{yz}y(1-p_y^2) - C_{xy}xp_x^2 - P_{xy}x(1-p_x^2)$$

3

Figure legends

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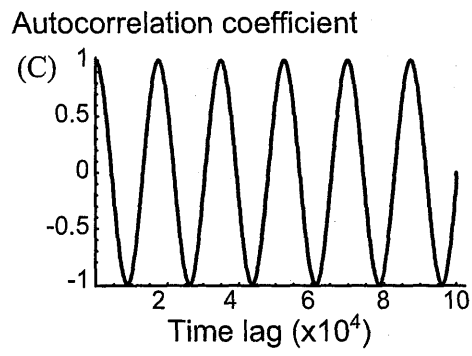
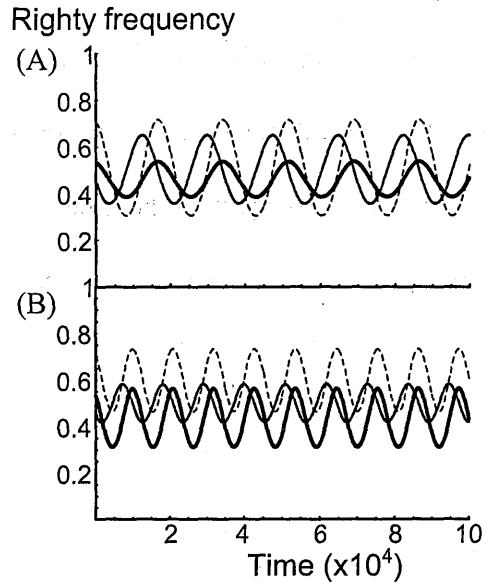
Fig. 1. Simulations of the gene frequency dynamics of a one-predator-two-prey model (Eq. 4). In panels 1A and 1B, the righty frequencies of x (p_x^2 : thin solid line), y (p_y^2 : broken line), and z (p_z^2 : thick solid line) are shown when six populations coexist. Panel 1C shows a correlogram of the whole simulation in 1A (all three species had a same correlogram). In panels 1A and 1B, predation efficiencies ($C_{xy}, P_{xy}, C_{xz}, P_{xz}$) are (0.15, 0.01, 0.15, 0.1) and (0.45, 0.03, 0.45, 0.03), respectively; and population sizes (x, y, z) are (9.31, 5.39, 1.55) and (5.57, 1.04, 1.56), respectively. Other parameters are: $m = 0.8, d_x = 0.5, e = 0, \alpha_1 = \alpha_2 = 0.1, r_y = 1.5, r_z = 2.0, K_y = 11.0, \text{ and } K_z = 5.0$.

1 Fig. 2. Simulations of the gene frequency dynamics of a one-predator-two-prey model
2 with genetic drift (Eq. 5). In panels 2A–2D, the righty frequencies of x (p_x^2 : thin solid
3 line), y (p_y^2 : broken line), and z (p_z^2 : thick solid line) are shown for the coexistence of six
4 populations. The genetic drift values ($\sigma_x, \sigma_y, \sigma_z$) used in panels 2A–2D are (2, 2, 2), (2, 2,
5 2), (5, 5, 5), and (2, 2, 1), respectively, with the time step $\Delta t = 0.001$. Panel 2E shows a
6 correlogram of the whole simulation in 2B (species x and y: broken line, z: solid line).
7 Other parameters used in 2A are $C_{xy} = C_{xz} = 0.15$, $P_{xy} = P_{xz} = 0.01$, $m = 0.8$, $d_x = 0.5$, $e = 0$,
8 $\alpha_1 = \alpha_2 = 0.1$, $r_y = 2.0$, $r_z = 1.0$, $K_y = 5.0$, and $K_z = 10.0$. The other parameters used in
9 panels 2B–2D are the same as those used in panel 1A (note that P_{xz} , r_y , r_z , K_y and K_z differ
10 from those of 2A).

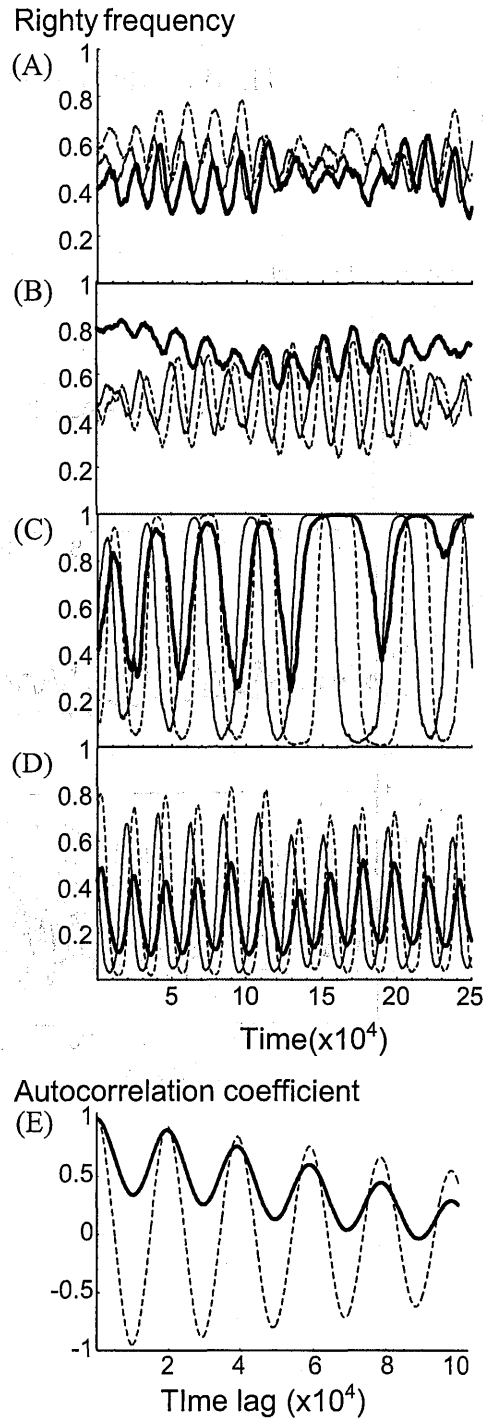
1 Fig. 3. Simulations of the gene frequency dynamics of a three-trophic-level system with
2 omnivory and with and without genetic drift (Eq. 6). The righty frequencies of x (p_x^2 :
3 thick solid line), y (p_y^2 : broken line), and z (p_z^2 : thin solid line) are shown for the
4 coexistence of six populations. The genetic drift values ($\sigma_x, \sigma_y, \sigma_z$) used in panels 3A–3C
5 are (0, 0, 0), (1, 1, 1), and (2, 2, 1), respectively, with the time step $\Delta t = 0.001$. Other
6 parameters are: $C_{xy} = 0.5, P_{xy} = 0.25, C_{xz} = 0.2, P_{xz} = 0.05, C_{yz} = 1.0, P_{yz} = 0.15, m = 0.8, d_x$
7 $= d_y = 0.5, r = 1.0,$ and $K = 5.0$.

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Fig. 1



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Fig. 2



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Fig. 3

