Labdien!

こんにちは
Kon nichi wa

I am Naota Ohsaki, PhD
of National Yamagata University, Japan.

I am a professor of Yamagata University in charge of International Exchange.

My mission is to stay at several Satellite Offices abroad of Yamagata University and to promote international exchange.

Satellite Offices Abroad of Yamagata University

(1) Hanoi University of Agriculture in Vietnam
(2) Yanbian University in China
(3) Jomo-Kenyatta University of Agriculture and Technology in Kenya
(4) Catolica University in Peru
(5) Gadjah Mada University in Indonesia
(6) Latvia University in Latvia

Where is Yamagata University

日本・Japan

北方領島
日本海
竹島
太平洋
尖閣諸島
大東諸島
小笠原諸島
南島島
沖ノ鳥島
排他的経済水域
公海

Japan is composed of 6852 islands.

Tokyo

1000km

Yamagata

Tokyo-Yamagata   Two and a half Hours by a Bullet Train
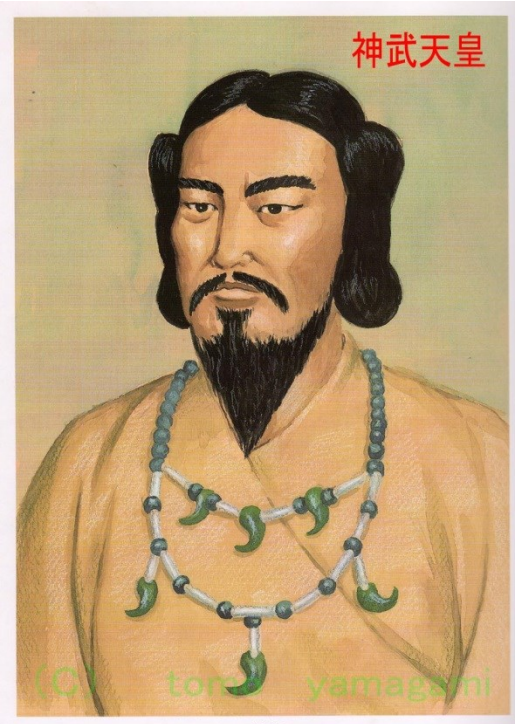

200km

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The symbol of Yamagata is cherry

神武天皇

**Around AC 250
Japan was united by
the first Emperor Jinmu.**

In 1192, Shogun, military commanders, robbed the political authority from the emperor and ruled Japan, though they were appointed by the emperor.

However, Japan was divided into 261 dominions ruled by feudal lords.

In 1868, Meiji Emperor, the 122nd generation, re-united Japan.

The 261 feudal dominions were converted to 47 prefectures ruled by governors elected by people.

Yamagata Prefecture is one of the 47 prefectures, and Yamagata city is the capital of Yamagata Prefecture.

In 1945, Emperor lost the real power of politics, and became a symbol of national integration.

Before 1945, there were 7 Imperial Universities in Japan, but after 1945 such universities were abolished and new national universities were established in each prefecture by integrating all national colleges and institutions in each prefecture.

The current emperor is the 125th generation.

The number of universities in Japan at present

National Universities	86
Public Universities (Prefecture, City)	82
Private Universities	603
Total	771

University ranking (Webometrics) of Yamagata University

In Japan : 31st

In the world : 766th

Yamagata University has six Faculties

Agriculture
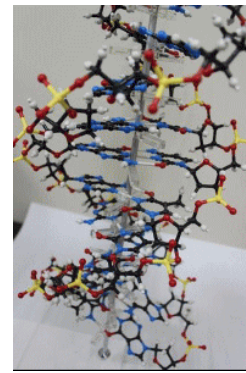

Science

Engineering

Medicine

Literature & Social Science

Education, Art & Science

Faculty of Science

Department of Mathematical Sciences
Department of Physics
Department of Material and Biological Chemistry
Department of Earth and Environmental Science
Department of Biology

Center for Accelerator Mass Spectrometry (AMS)
Radioisotope Laboratory
Urabandai Limnological Station

Department of Biology

12 Laboratories, 6 Fields

Phylogenetic
  Phylogenetic
  Coevolution
Evolution and Genetics
  Ecological genetics
  Evolutionary genetics
Ecology
  Plant ecology
  Animal Ecology

Plant Physiology
  Plant physiology
  Algae growth physiology
Animal Physiology
  Behavioural physiology
  Comparative biochemistry
Developmental Biology
  Experimental morphology
  Reproductive biology

Faculty of Agriculture, six courses

(1) **Safe and Reliable Agricultural Production**

(2) **Management of Food, Agriculture and Environment**

(3) **Food and Applied Life Sciences**

      Molecular and cellular biochemistry, Control of fermentation, Applied microbiology, Biomass utilization, Animal reproduction

(4) **Plant and Bio-resource Sciences**

      Bioorganic chemistry, Plant genetics and breeding, Post-harvest physiology, Plant genetic resources, Plant nutrition and soil science, Utilization of microbial resources

(5) **Forest Science**

(6) **Water and Land Environment Science**

International Programs | **In Japanese or English**

Undergraduate and Graduate

Degree Programs | **Regular programs of each Department**

B: 4 years, M: 2 years, PhD: 3 years

Short-term Study, Exchange Program | **Regular Programs of each Department, Japan Studies Programs**

One year or Half

Graduate

Research Programs | **Under an academic advisor**
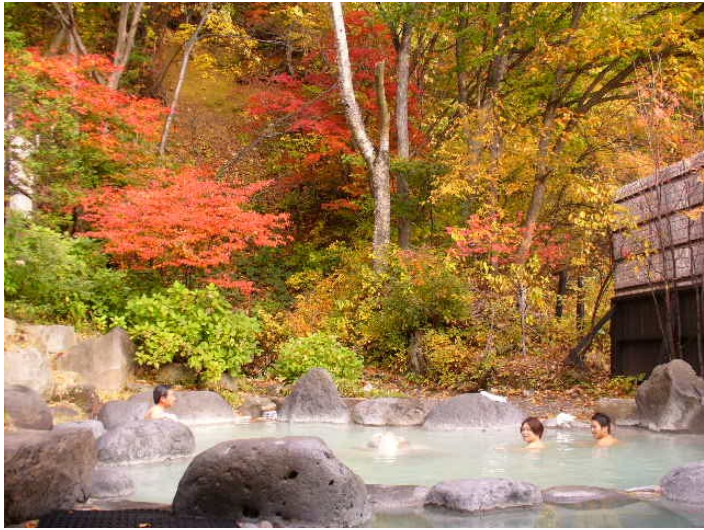
One year or Half

Life in Yamagata

Today, I will introduce my study.

My major is Evolutionary Ecology of Insects, which makes ecology and behaviour of insects clear from the viewpoint of evolution.

Food-Plant Choices Determined by Competitive Exclusion Between Closely Related Butterflies

Naota Ohsaki
Yamagata University,
Japan

The competitive exclusion principle states that no two species can coexist, if they occupy the same niche and compete for the same resources (Gause 1932).

Therefore, one species needs to evolve into a slightly different niche in order to end interspecific competition.

These are predicted by a number of mathematical and theoretical models.

However, directly competitive exclusion is rarely observed in natural ecosystem.

In particular, interspecific competition in phytophagous insect communities like butterflies is thought negatively (Lowton and Strong 1981), though indirect competition is suggested (Chesson and Huntley 1997 *).

Here we show that two closely related butterfly species, *Pieris napi* and *P. melete,* compete to use more suitable food-plants, and smaller *P. napi* would have completely excluded larger *P. melete* from them.

Pieris napi

Pieris melete

In the association between herbivorous insects and their food-plants, many closely related herbivorous insects share taxonomically similar plant species each other (Kuno 1992).

In Kyoto, west Japan, different butterfly species of the same genus *Pieris* uses the different plant genus of the same family Brassicaceae, each other.

Kyoto Univ

Maiko

Kyoto

Kinkakuji

Kiyomizudera

In Kyoto, western Japan, different butterfly species of the same genus *Pieris* uses the different plant genus of the same family Brassicaceae, each other.

Pieris rapae
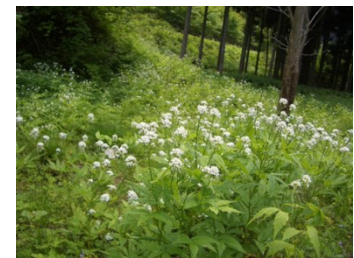

Pieris napi

Pieris melete

Genus *Brassica*

Genus *Arabis*

Genus *Cardamine*

This relationship is often explained by phylogenetic association between insects and plants.

However, phylogenetic congruence is rarely found in insect-host plant systems, and consequently, co-speciation of associated lineages is not likely to explain patterns of insect-plant associations (Smiley 1987).

The food-plant choice of herbivorous insects should be determined to enhance their ecological fitness.

At that time, it may be more a function of interactions with natural enemies via enemy-free space allowing insects to escape most natural enemies than of host plant chemistry (Faeth 1992).

Fitness = No. of eggs x survival until reproductive age x 1/2

No. of eggs means that total number of eggs laid by one female in her life .

The production of fertilized eggs is collaboration with females and males.

Therefore, ecological fitness means the total number of mature offspring per individual.

If fitness > 1, such offspring will prosper.
If fitness < 1, such offspring will decline.

In the case

The number of eggs laid: 200
Survival rate: 0.05% (0.005)
Fitness = 200 x 0.005 x ½ = 0.5

Its offspring will decline.

There are two ways to enhance the fitness from 0.5 to 1.
(1) Increase of the number of eggs laid.
(2) Increase of the survival rate.

Increase of the number of eggs laid :
200 → 400
Survival rate: 0.5% (0.005) → 0.5% (0.005)
Fitness = 400 x 0.005 x ½ = 1

Increase of survival rate:
0.05% (0.005) → 0.1% (0.01)
The number of eggs laid: 200 → 200
Fitness = 200 x 0.01 x ½ = 1

200 x 0.005 = 1 → 200 x 0.01 = 2

When one more larva can survive, they can enhance their fitness from 0.5 to 1.

Therefore, use of food-plants forming

"enemy free space"

is very effective to enhance their fitness for phytophagous insects.

Competition may provide a selective force resulting in different patterns of resource use between the species.

Connell (1983) referred to this evolutionary effect as the ghost of competition past.

Certainly, we cannot go back in time to determine whether the species once competed more strongly than at present.

However, our data show such probabilities.

Around 1960, a cruciferous plant *Rorippa sylvestris* invaded into Hokkaido Island, northern Japan, probably with pasture seed (Osada 1972).

Rorippa sylvestris

Hokkaido Island

Hokkaido Island

Hokkaido Univ

Sapporo City

Wheat

Snow

Lavender

The first record about the relationship between naturalized plant *R. sylvestris* and *Pieris* butterflies documented that both *P. napi* and *P. melete* laid eggs on *R. sylvestris* (Hasegawa 1966).

However, at present, only *P. napi* uses *R. sylvestris*. *P. melete* uses only an indigenous plant *Cardamine leucantha*.

R. sylvestris

C. leucantha

We attempted to explain their food-plant use in the directly interspecific competition.

To assess the relative suitability of naturlized plant *R. sylvestris* and indigenous one *C. leucantha* for the *Pieris* butterflies, we first measured the pupal masses fed on them.

	P. napi		**P. melete**	
	n	Mass (mg)	n	Mass(mg)
R. sylvestris	12	184.3±18.7	12	238.2±8.2
C. leucantha	15	132.4±26.1	14	187.5±25.3

The naturalized food-plant *R. sylvestris* was an intrinsically superior food-plant for both *P. napi* and *P. melete*.

Secondly, I documented the parasitism rates of *Pieris* larvae on each cruciferous plant in six areas, which were divided into two types.

(1) The areas where *R. sylvestris* and *C. leucantha* grew in adjacent patches (A-C).

(2) The areas in the cores of forest of deciduous trees in national parks without naturalized plants *R. sylvestri*s (D-E).

Larvae of *Pieris* butterflies have two types of parasitic natural enemies.

（1）**Wasp: *Cotesia glomerata***

（2）**Tachinid flies**

They lay eggs in the larval bodies of *Pieris* butterflies, and their final instar larvae egress from the host bodies.

Susceptible stages of *Pieris* butterflies to oviposition by parasitoids and the stages that parasitoids emerge from.

Pieris butterflis Egg L1 L2 L3 L4 L5 Pupa Adult

C. glomerata ————— ●

Tachinid flies ———— ●

oviposition emergence
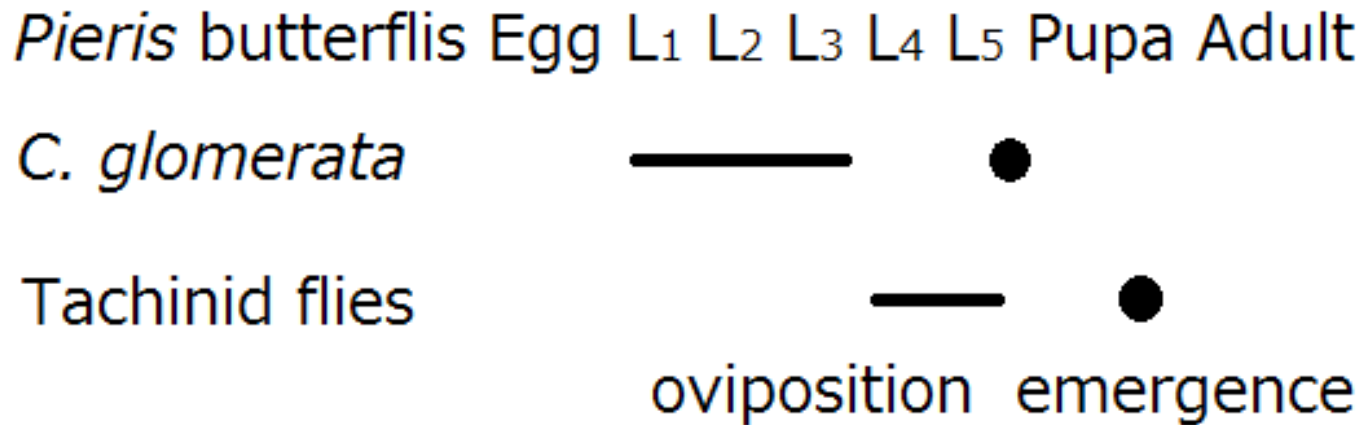
When the both parasitoids lay eggs in the same body of the host, *C. glomerata* larvae always win the inter-specific competition with Tachinid larvae.

However, *C. glomerata* eggs laid into *P. melete* larvae are killed by haemocytic encapsulation.

Parasitism rates of *P. napi* and *P. melete* by wasp *C. glomerata* and Tachnid flies.

We collected only 5th instar larvae.

	plant	No. of shoots	n	*P.* % wasp	*napi* % flies	% total		n	*P.* % wasp	*mel* % flies	*ete* % total	
A	Rs	3000	21	0	0	0	a/A	0				
	Cl	2000	0					27	3.7	63	66.7	bc
B	Rs	3000	24	0	12.5	12.5	a/A	0				
	Cl	2000	0					23	4.3	52.2	56.5	bc
G	Rs	3000	22	4.5	19.2	22.7	ab/A	0				
	Cl	2000	0					18	0	61.1	61.1	bc
D	Cl	2000	22	0	77.3	77.3	B	0				
E	Cl	2000	21	61.9	33.3	95.2	B	0				
F	Cl	2000	22	59.1	27.2	86.3	B	0				

Different letters are significantly different ($p < 0.0033$)

Thus, at present, only *P. napi* uses *R. sylvestris*.

P. melete uses only an indigenous plant *Cardamine leucantha*, which is ubiquitously distributed in forests on Hokkaido Island, even in areas where *R. sylvestris* is distributed in adjacent places (census areas A–C).

In such areas *P. napi* uses only *R. sylvestris*.

On the other hand, at the core of wide forests in the national parks, *R. sylvestris* is not distributed and only *C. leucantha* is distributed (census areas D-F).

In such areas, we could find many *P. napi* butterflies and a few *P. melete* butterflies flying, and we could collect only *P. napi* larvae from *C. leucantha*.

Parasitism rates of *P. napi* and *P. melete* by wasp *C. glomerata* and Tachnid flies.

We collected only 5th instar larvae.

	plant	No. of shoots	n	P. napi % wasp	% flies	% total		n	P. melete % wasp	% flies	% total	
A	Rs	3000	21	0	0	0	a/A	0				
	Cl	2000	0					27	3.7	63	66.7	bc
B	Rs	3000	24	0	12.5	12.5	a/A	0				
	Cl	2000	0					23	4.3	52.2	56.5	bc
G	Rs	3000	22	4.5	19.2	22.7	ab/A	0				
	Cl	2000	0					18	0	61.1	61.1	bc
D	Cl	2000	22	0	77.3	77.3	B	0				
E	Cl	2000	21	61.9	33.3	95.2	B	0				
F	Cl	2000	22	59.1	27.2	86.3	B	0				

Different letters are significantly different ($p<0.0033$)

In the three areas (A-C) with *R. sylvestris* and *C. leucantha*, *P. napi* larvae were collected from only *R. sylvestris* and were parasitized by wasp *C. glomerata* (3.0%) and tachinid flies (10.2%) with a mean total parasitism rate of 11.7%.

P. melete larvae were collected from only *C. leucantha* and were also parasitized by both *C. glomerata* (2.7%) and tachinid flies (58.8%) with a mean total rate of 61.7%.

Usually *C. glomerata* eggs laid into *P. melete* larvae are killed by haemocytic encapsulation (Sato 1976).

In the other three areas (D-F) without *R. sylvestris*, *P. napi* were collected from *C. leucantha*, and were parasitized by both *C. glomerata* (40.3%) and tachinid flies (45.9%) with a mean total parasitism rate of 86.2%.

No *P. melete* larvae were observed.

In conclusion,
the mean parasitism rate of *P. napi* on
R. sylvestris was lower than that of *P. napi*
and *P. melete* on *C. leucantha*.

We could not determine the
mechanism causing low parasitism on
R. sylvestris, but we could have easily
inferred that *R. sylvestris* forms **enemy
free-space** by its dense colonies.

Thus,
***R. sylvestris* must be more suitable than *C. leucantha* for both *P. napi* and *P. melete*, but only *P. napi* uses *R. sylvestris*.**

To analyse differences in food-plant choice by *P. napi* and *P. melete* among the six areas, we examined the ratio of the number of eggs laid on *C. leucantha* to the total number of eggs laid on both plants in portable field cages.

{Eggs on C. leucantha / (Eggs on *C. leucantha* + Eggs on *R. sylvestris*)} x 100

Number of females of *Pieris* butterflies in each range of frequencies of number of eggs on *C. leucantha* per total number of eggs on *C. leucantha* and *R. sylvestris* laid in the field cages.

	Pieris napi						*Pieris melete*					
Census Area	**A**	**B**	**C**	**D**	**E**	**F**	**A**	**B**	**C**	**D**	**E**	**F**
Sample Size	14	10	25	24	23	27	12	10	2	10	12	12
Composition test	a	a	ab	bc	c	c	a	ab	ac	c	bc	c
% Oviposition												
x = 0%	14	10	6	0	0	0	0	0	0	1	0	0
0%< x≦20%	0	0	11	10	6	3	0	0	0	1	0	3
20%< x≦40%	0	0	4	7	7	7	0	0	0	1	1	0
40%< x ≦60%	0	0	3	2	4	6	0	0	0	1	1	0
60%< x ≦80%	0	0	1	5	4	8	0	0	0	0	1	3
80%< x <100%	0	0	0	0	2	3	0	0	1	1	6	4
x = 100%	0	0	0	0	0	0	12	10	1	3	3	2

Among different census areas, different letters show significantly different food-plant choice (p < .05)

The oviposition tendencies of both *Pieris* species differed among the areas.

P. napi collected from the two areas (A-B) with both *R. sylvestris* and *C. leucantha* chose only *R. sylvestris*, but *P. melete* collected there chose only *C. leucantha*.

On the other hand, both *P. napi* and *P. melete* collected from three areas (D-F) without *R. sylvestris* chose both *R. sylvestris* and *C. leucantha* equally.

One other area (C) contained both *C. leucantha* and *R. sylvestris* in adjacent paches, but the forest containing *C. leucantha* extended to the forest core in a national park.

Both *P. napi* and *P. melete* from there had an intermediate tendency.

Presumably, this area was a spatio-temporally transitional zone.

Novel plants are often acceptable when encountered (Ohsaki ans Sato 1999), and many novel plants have been used by indigenous herbivorous insects (Duncan and Williams 2002).

These facts suggest that after around 1960, when a   more suitable food-plant *R. sylvestris* invaded into Hokkaido Island, *P. napi* began to use the naturalized food-plant *R. sylvestris* and lost its preference for the indigenous food-plant *C. leucantha*.

On the other hand, *P. melete* once used the potential food-plant *R. sylvestris*, and has lost its preference for it in areas where both butterflies usually encounter both plants.

These phenomena imply a probability of the occurrence of past competition between *P. napi* and *P. melete*.

To examine the probability that *P. napi* has directly excluded *P.melete* from more suitable food-plants, we released adult butterflies of *P. napi* and *P. melete* simultaneously in a butterfly house of Itami city, and observed their behaviour for three active days.
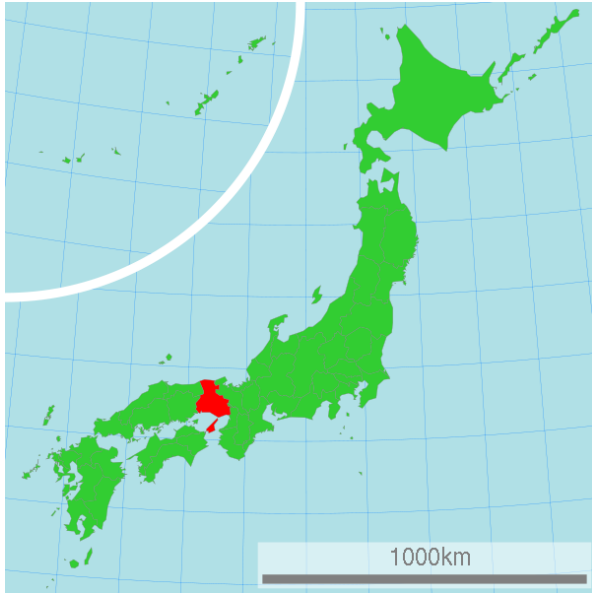
Itami City

Butterfly House

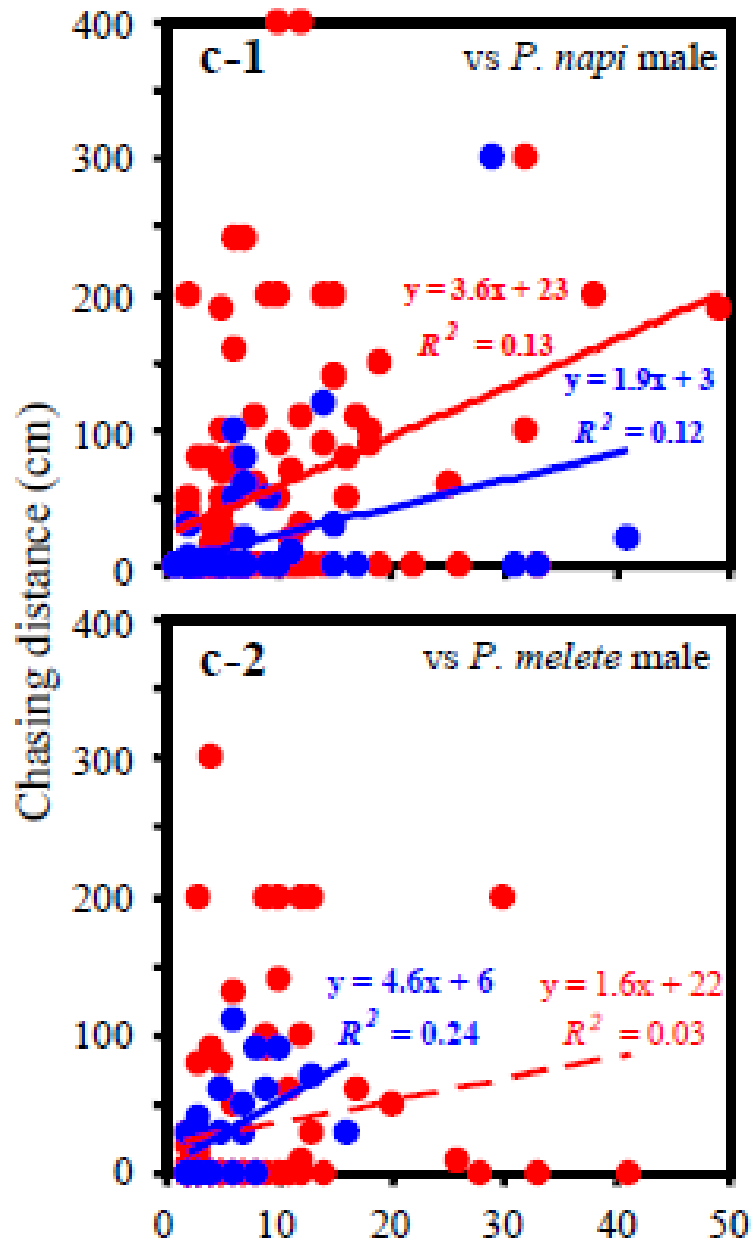*P. napi* males courted females more frequently than *P. melete* (Fig. a).
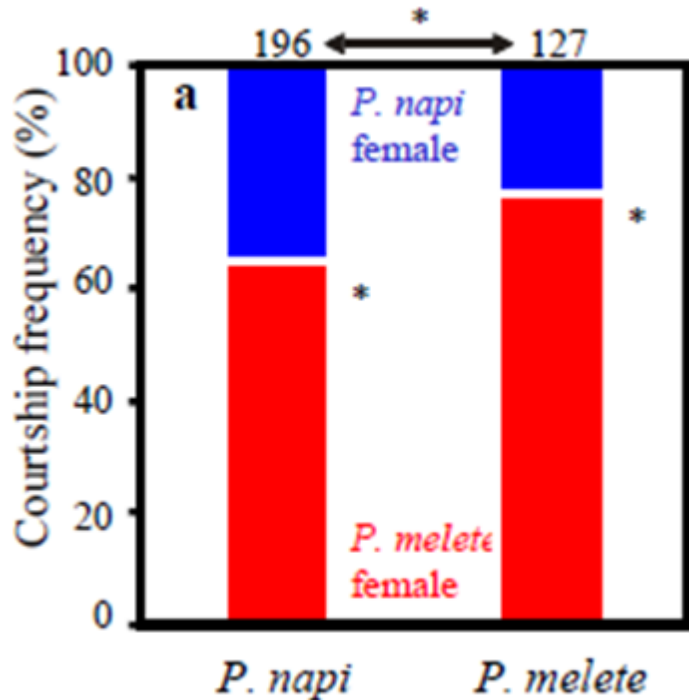
At that time, not only *P. melete* males but also *P. napi* males preferred *P. melete* females (Fig. a), probably because males preferred larger females.

In general, males should mate with larger females with more eggs to enhance their ecological fitness.
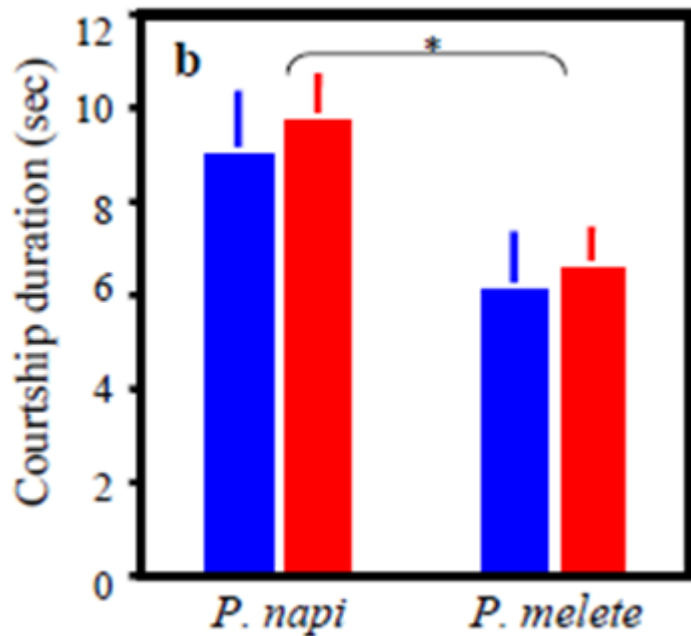
P. napi males lasted longer courtship than *P. melete* males (Fig. b), but the duration of their courtship were not different between to *P. napi* and to *P. melete* (Fig b).

c-1 vs *P. napi* male

$y = 3.6x + 23$
$R^2 = 0.13$

$y = 1.9x + 3$
$R^2 = 0.12$

Chasing distance (cm)

c-2 vs *P. melete* male

$y = 4.6x + 6$
$R^2 = 0.24$

$y = 1.6x + 22$
$R^2 = 0.03$

When males courted females, females frequently escaped and males chased them for some distance.

In such cases, *P. napi* males chased *P. melete* females longer distance than any combination of the male and the female (Fig. c).
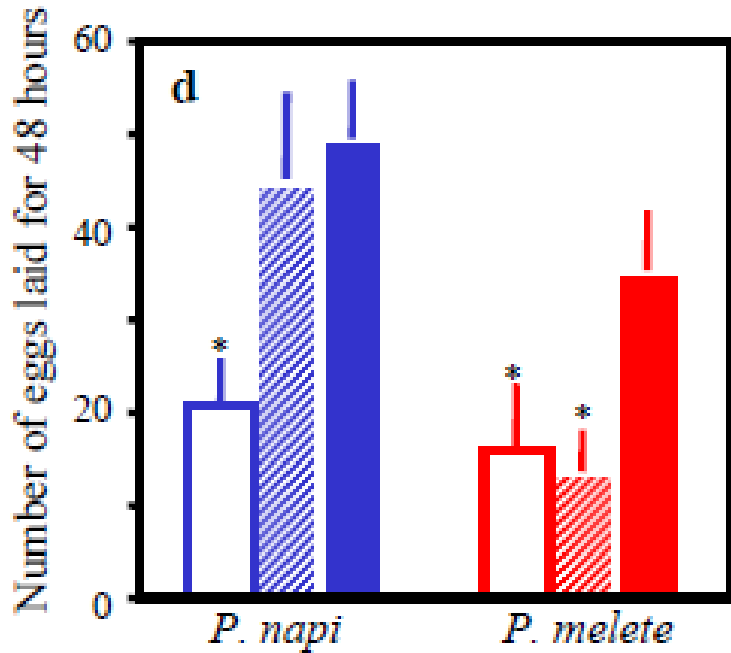
As a result, smaller *P. napi* males drove out larger *P. melete* females more frequently from the resources.

To evaluate what influence the difference of courtship between *P. napi* and *P. melete* gives their fitness, each female was introduced into the field cage with either a male of *P. napi* or *P. melete*.

We examined their number of eggs laid.

d

Number of eggs laid for 48 hours

P. napi   *P. melete*

Left: with an intra-specific male.

Middle: with an inter-specific male.

Right: With no male.

An intra-specific male obstructed a female to lay eggs through his courtship for both *P. napi* and *P. melete,* and the number of eggs laid was reduced by half.

In addition, *P. napi* male also reduced the number of eggs laid by *P. melete* by half. However, *P. melete* male did not influence *P. napi* female.

That is, when they coexist, the fitness of *P. melete* decreases more and more.

Oppositely, the fitness of *P. napi* may increases, because the concern of *P. napi* males turn to *P. melete* females.

Therefore, if *P. melete* retains its fitness, *P. melete* must shift towards different host food-plants which *P. napi* does not use.

In west Japan, Kyoto, *P. napi* and *P. melete* use different indigenous cruciferous plants: *P. napi* uses intrinsically inferior *Arabis* plants, whereas *P. melete* uses intrinsically superior *Cardamine* plants. These plants form exclusive patches.
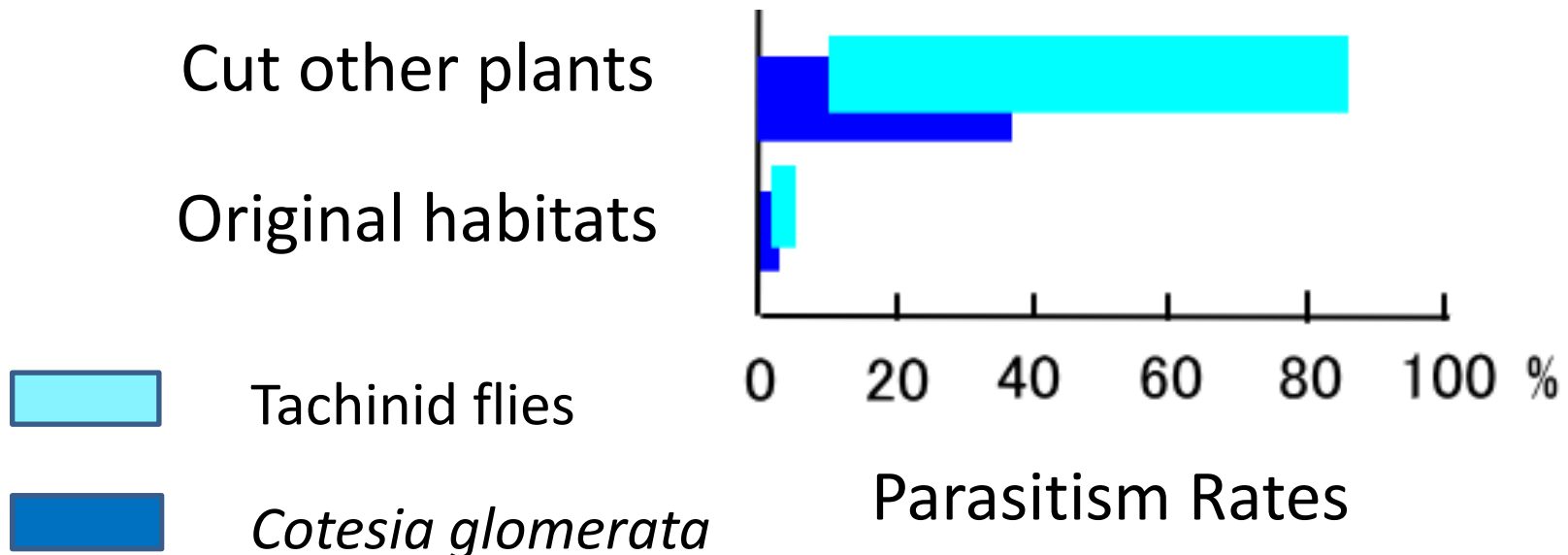

Kyoto

Arabis

Cardamine

P. napi has no physiological defence mechanism against wasp *C. glomerata*, but *P. melete* can kill its eggs by encapsulation.

Therefore, we once thought *P. napi* used intrinsically inferior *Arabis* plants because of their forming enemy free-space, and *P. melete* used intrinsically superior *Cardamine* plants because of its physiological defence (Ohsaki and Sato 1994)

However, *P. melete* was heavily parasitized by tachinid flies (76%), so plants forming enemy free space must be more suitable than intrinsically superior plants not forming enemy free space even for *P. melete*.

P. napi and *P. melete* can reach adulthood raised on both *Arabis* plants and *Cardamine* ones.

However, in field cages, they avoid other's food-plants each other, although they laid eggs on various potential food-plants that did not occur in their natural habitats (Ohsaki and Sato 1999).

1 *B. oleracea*
2 *B. pekinensis*
3 *R. sativus*
4 *Cardamine a.*
5 *Arabis g.*
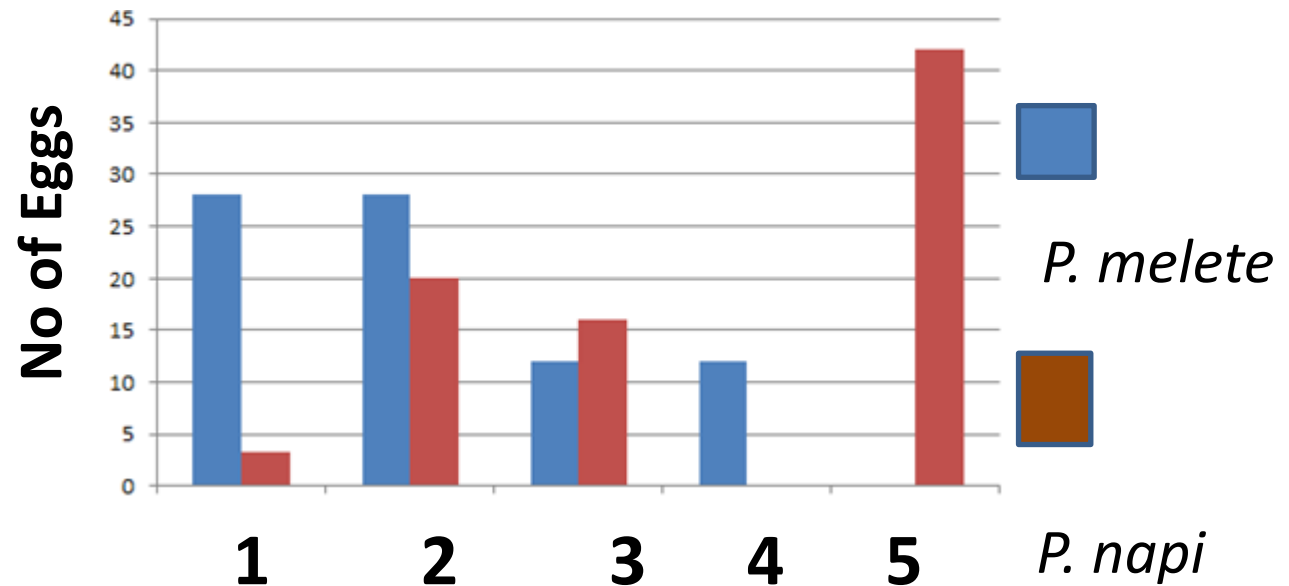
P. melete

P. napi

This implies that in the past, both *P. napi* and *P. melete* may have laid eggs on both *Arabis* plants and *Cardamine* plants, but have currently lost their preference for laying eggs on one type of plants.

Thus, the same logic can adjust to explain this phenomenon as that in Hokkaido Island.

That is, smaller *P. napi* directly excluded larger *P. melete* from *Arabis* plants because of mating interference.

In nature, many closely related herbivorous insects segregate on taxonomically close plant species.

Most cases of this relationship are apt to be explained by phylogenetic association between insects and plants.

If this relationship can be analysed from the view of mating interference, we may gain new insight into food-plant choice by herbivorous insects.

Acknowledgements

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