# Insect host preference: its definition, correlates and evolutionary dimensionality

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# Why is host **USE** by herbivorous insects important?

1) It mediates transmission of diseases of plants and animals

2) Its changes create novel pests and novel community interactions

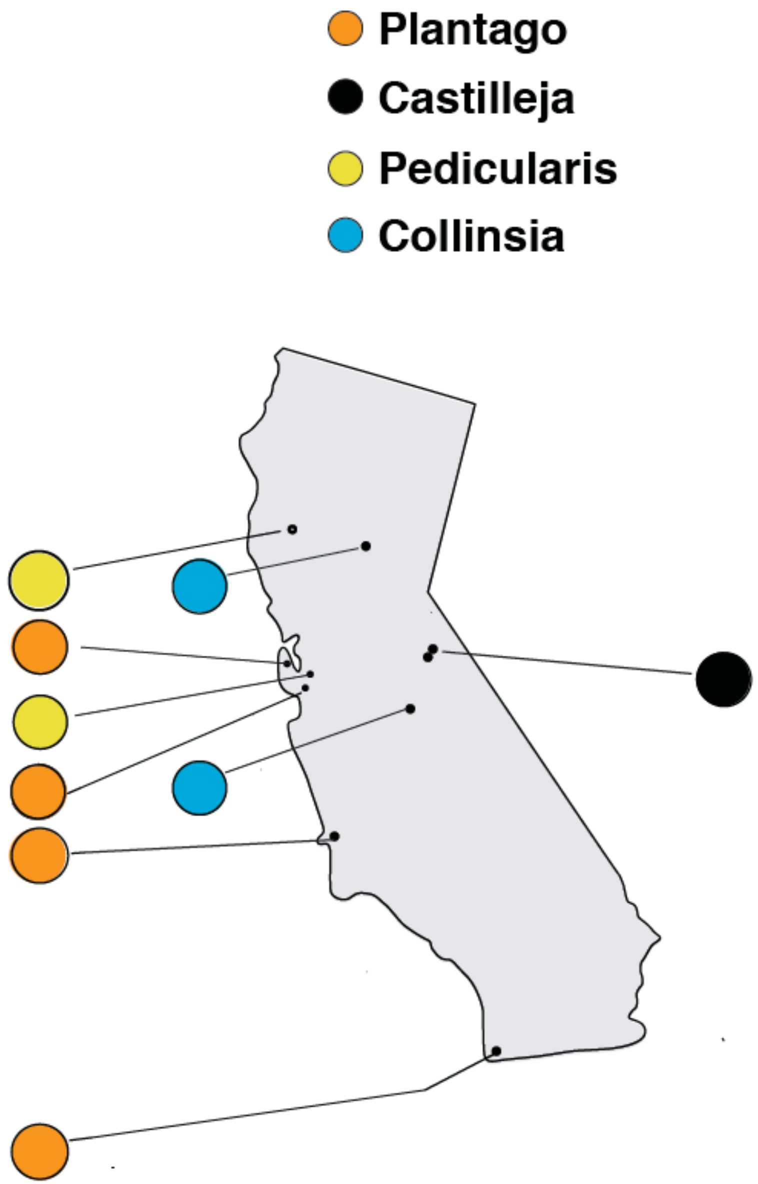
3) use of different hosts can impede gene flow and assist ecological speciation

4) Conservation planning requires understanding host and habitat requirements

I started recording geographic variation of diet and oviposition preferences of Edith's Checkerspot butterfly in 1968.

9 populations collectively used four host genera but each population was monophagous.

When tested in a greenhouse, They had different **oviposition preferences**. (Singer 1971 Evolution)




GEOGRAPHIC VARIATION OF DIET IN EDITH'S CHECKERSPOT BUTTERFLY
(SINGER, EVOLUTION, 1971)

THEN I found a population in which 40% of the larvae were on *Plantago* and 60% on *Castilleja*.

I assumed that their mothers had different preferences so I conducted an experiment to ask whether this difference was cultural or genetic

It failed, the larvae all died.

LATER I discovered that and larvae can move between these small plants and that each larva was doing 40% of its feeding on *Plantago* and 60% on *Castilleja*.

They were not variable in behaviour. I had wasted my time on a non-question

I learned more than 50 years ago that insects feeding on different hosts don't necessarily have different preferences.

But what matters most in practice is HOST USE - what insects DO, not what they PREFER

So why and how is preference important? How does it relate to observed patterns of host use?

# Preference: its definition, correlates and evolutionary dimensionality

When they say **"preference,"** ecologists usually mean the use of resources in relation to their abundance. For example, "the proportion of food items in the diet as a function of their availability in the habitat? (Hassell & Southwood 1978 Annu Rev Ecol Syst).

By contrast, behaviourists usually mean the set of probabilities of accepting specific resources that are encountered.

What’s the difference between the ecological and behavioural concepts of preferece?

Imagine two hosts of equal overall density, but one with a clumped distribution and one with a regular distribution.

Imagine an insect that starts oviposition searches at random points and has no behavioural preference, being equally likely to accept the two hosts after encounter


The insect will encounter the clumped host (blue)
less frequently than the regularly-distributed host (green).

By the ecological definition the randomly-behaving insect prefers the regularly-distributed host, although by the behavioural definition it has no preference.

(Singer 2000 Ecology Letters)

Accumulation of eggs on isolated plants has been described by ecologists as a preference for those plants

(Kareiva)

We found butterflies that preferred isolated plants by the ecological definition and plants in clumps by the behavioural definition (Mackay & Singer 1982 Ecol Ent) .

Which concept to use?  If we are interested in evolution the behavioural concept is more useful because it can be **defined** as a trait of the insect, while the ecological concept is better seen as a trait of the plant-insect interaction.

Traits of the insect have heritabilities, can be targets of selection and can evolve.

The literature is confused about what are traits of insects and of plants. For example, the standard definition of induced plant responses is "changes in the plant that affect insect preference or performance." (Karban & Myers 1989, Annu Rev Ecol Syst 20, 331> CITED 625 TIMES; Agrawal 1998 Science 279:1201>)

The insect is not changing in this scenario, it either prefers induced plants or it does not. This definition is confused! (Singer 2000 Ecology Letters)

I have suggested these definitions (Singer 2000 Ecology Letters) :

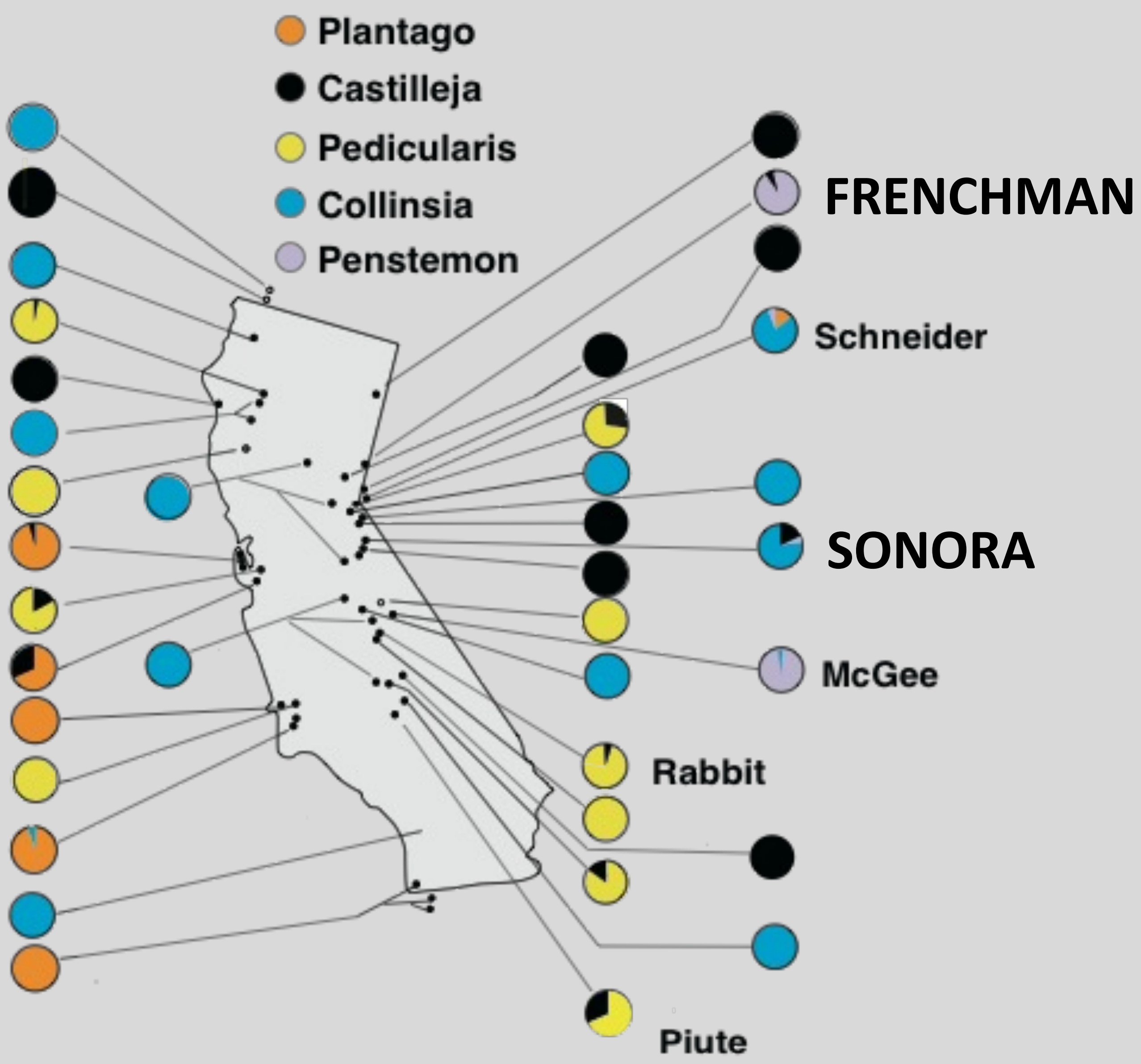
1) "preference" as an insect trait is the set of likelihoods of the insect accepting specified plants that are encountered

2) "acceptability" as a plant trait is the set of likelihoods of a plant being accepted for feeding or oviposition by a specified insect or set of insects that encounter it.

## Can we design experiments to ask how variation of insect preference and host acceptability interact?

YES but it requires careful experimental design. I'll describe four experiments.

First, using Edith's checkerspot butterfly, we compared insects and plants from two sites with near-identical plant communities but different insect-plant associations.




# A spatial pattern of plant-insect association

Proportions of eggs laid on each plant genus by Edith's checkerspot

Singer 1971 Evolution
Singer & Parmesan 1993 Nature
Singer & McBride 2012 Ecology

## What was the mechanism causing butterflies at Frenchman to use *Penstemon rydbergii* and those at Sonora to use *Collinsia parviflora?*

(1) We offered butterflies plant pairs of *Penstemon* & *Collinsia* at their home sites. Frenchman butterflies all preferred *Penstemon* (n = 23) and Sonora butterflies, with ONE exception, preferred *Collinsia* (n = 18)

2) When offered plant pairs of *Penstemon* & *Collinsia*, from the other site, Frenchman butterflies continued to prefer *Penstemon* (n = 22) but Sonora butteflies gave mixed results: 8 preferred *Penstemon,* 10 preferred *Collinsia.*

3) When offered plant pairs of Frenchman and Sonora *Penstemon*, butterflies from both sites either preferred the plant from Frenchman (n = 38) or showed no preference(n = 8); None preferred Sonora. (Singer & Parmesan 1993 Nature)

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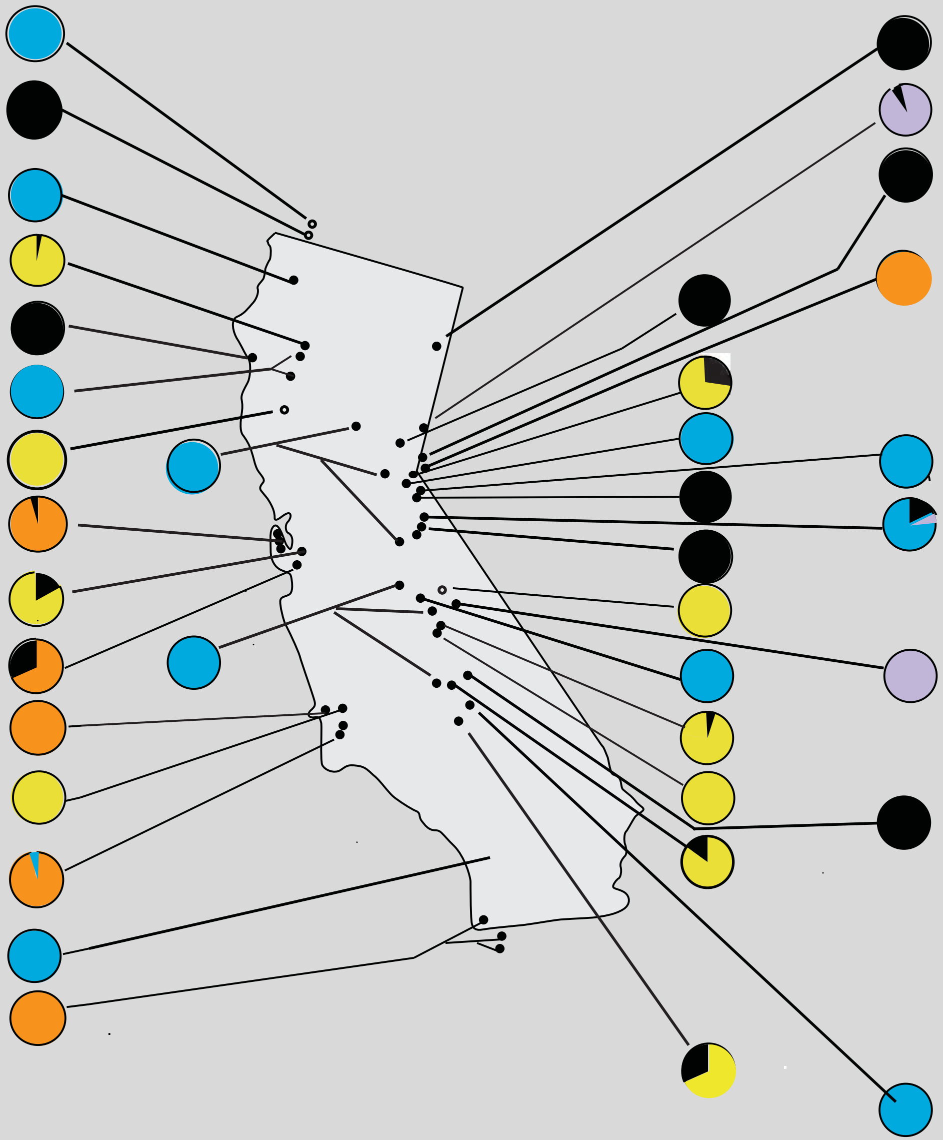
# How do variation of insect preference and host acceptability interact?

The difference in acceptability between *Penstemon rydbergii* from the two sites was preserved when plants were grown from seed in the greenhouse in BOTH soil origins.

The difference in preference between *Euphydryas editha* butterflies from the two sites was preserved when insects were raised from the egg on a common host, *Collinsia.*

(Singer & Parmesan 1993 Nature)

Singer 1971 Evolution
Singer & Parmesan 1993 Nature
Singer & McBride 2012 Ecology
Singer & Parmesan 2021 GCB
Parmesan & Singer 2022 Phil Trans



- **Plantago**
- **Castilleja**
- **Pedicularis**
- **Collinsia**
- **Penstemon**

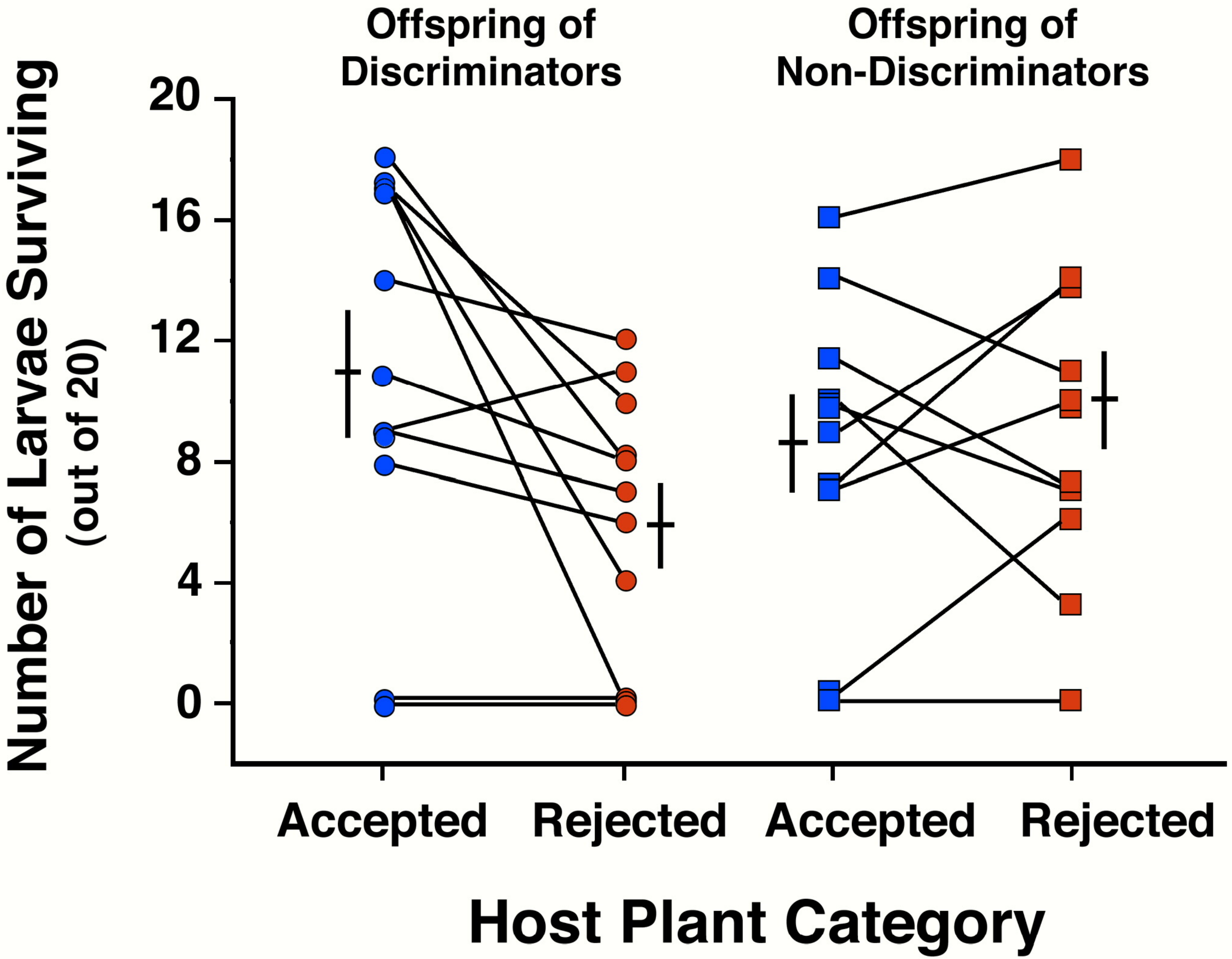
Proportions of eggs laid on each plant genus by Edith's checkerspot butterfly

## Second experiment asking how variation of insect preference and host acceptability interact

At a site, Rabbit Meadow, where *Pedicularis semibarbata* was the principal host, some butterflies discriminated among individual *Pedicularis*, while others did not. All discriminations were in the same direction: **variable preference**.

Some *Pedicularis* plants were acceptable to discriminating butterflies, some were not: **variable acceptability.**

We measured survival of offspring of the two classes of butterfly on the two classes of plant.




David Ng
Nature
1988

Ilkka Hanski with his title and coat of arms



*Ilkka 1, Dei Gratia cinxiarum Rex*

# Third experiment asking how variation of insect preference and host acceptability interact

*Melitaea cinxia* butterflies in a large Finnish metapopulation (1.6 kilopatches) use two hosts: *Veronica* and *Plantago.*

We raised separate cultures in Texas from a *Veronica*-using patch and a *Plantago*-using patch.

# Third experiment asking how variation of insect preference and host acceptability interact

We asked all the the butterflies to rank THE SAME 6 plants, 3 *Veronica* and 3 *Plantago,* chosen for diversity of acceptability.

**Half the butterflies from the *Veronica* patch ranked all 3 *Veronicas* over all 3 *Plantagos*.  None ranked all the *Plantagos* over all the *Veronicas***

**Half the butterflies from the *Plantago* patch ranked all 3 *Plantagos* over all 3 *Veronicas*.  None ranked all the *Veronicas* over all the *Plantagos*.**

(Singer & Lee 2000 Ecology Letters)

**BUT what about the other half? They did not rank the plants taxonomically. They told us that THIS *Veronica* is better than THAT *Plantago* but THIS *Plantago* is better than THAT *Veronica*.**

**So some butterflies responded more to variation between the host genera, while others responded more to variation within host populations.**

**In our paper we argue that in some experimental designs this type of complexity could cause insects to be recorded as variable in preference for host species when they are not. Variation within host populations can masquerade as variation among host species**

(Singer & Lee 2000 Ecology Letters)

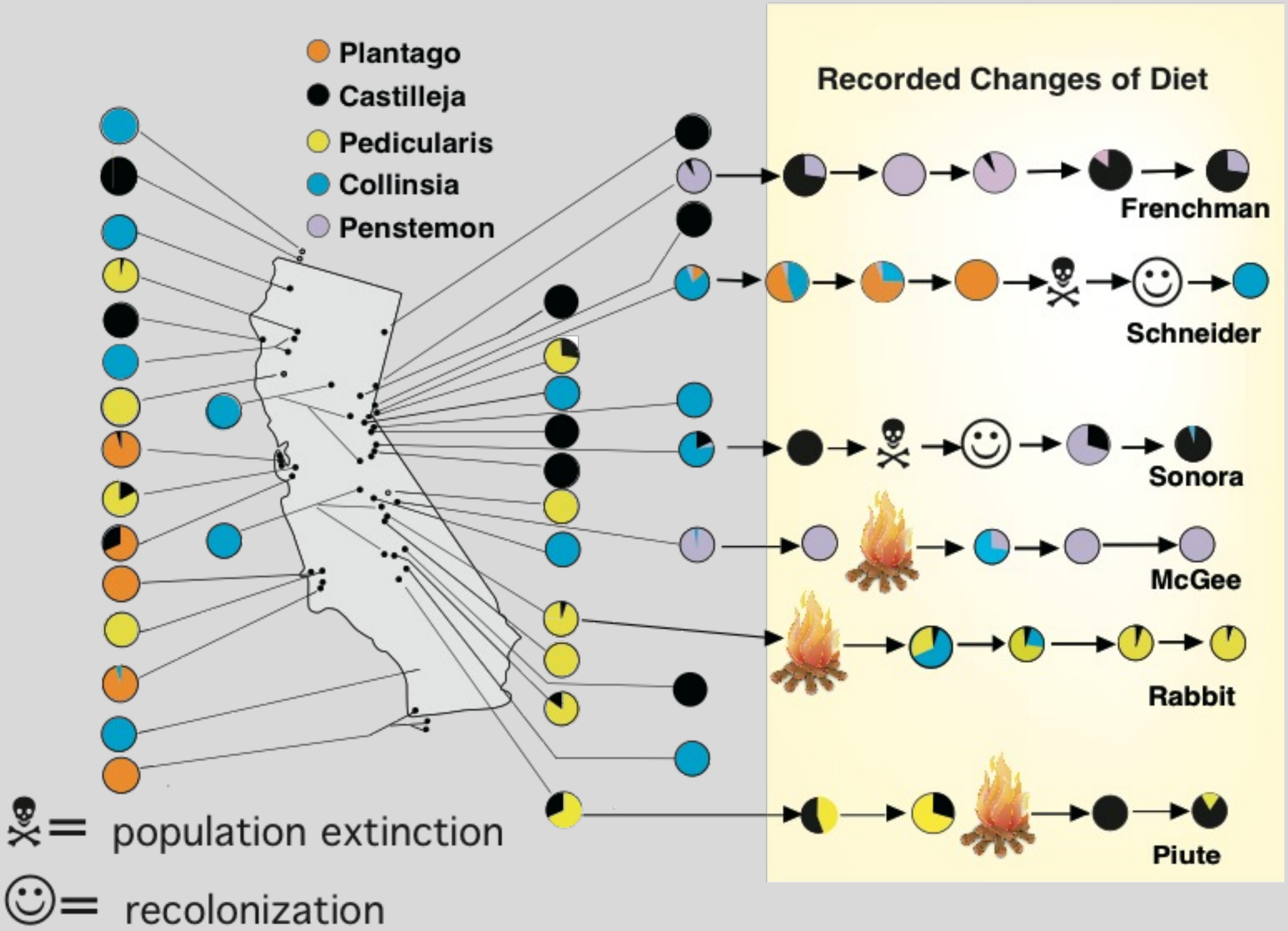
# FOURTH experiment asking how variation of insect preference and host acceptability interact

**We found a practical example in which choice of plants to represent their species changed which species was preferred.**

***Euphydryas aurinia*** **on Pic St Loup oviposits on** ***Cephalaria*****. Over much of its range it uses** ***Succisa*****. Robert Mazel in Perpignan reported that all populations prefer** ***Succisa*****, no matter what host they use.**

**When we chose** ***Cephalaria*** **plants at random, we found that Mazel was right, the butterflies preferred** ***Succisa*****, a plant that did not grow in their habitat. They seemed to waste time searching for a nonexistent host.**

**When we tested individual** ***Cephalaria*** **that had been chosen,** ***Succisa*** **was no longer preferred.** Singer et al. Ecology Letters 2002




Singer & Parmesan 2018
Nature

Singer & Parmesan 2021
Global Change Biology

Singer & Parmesan 2019
Evol. Appl

# Insect host preference: its definition, correlates and evolutionary dimensionality

Preference was not correlated with fecundity (Agnew & Singer 2000 Oikos).

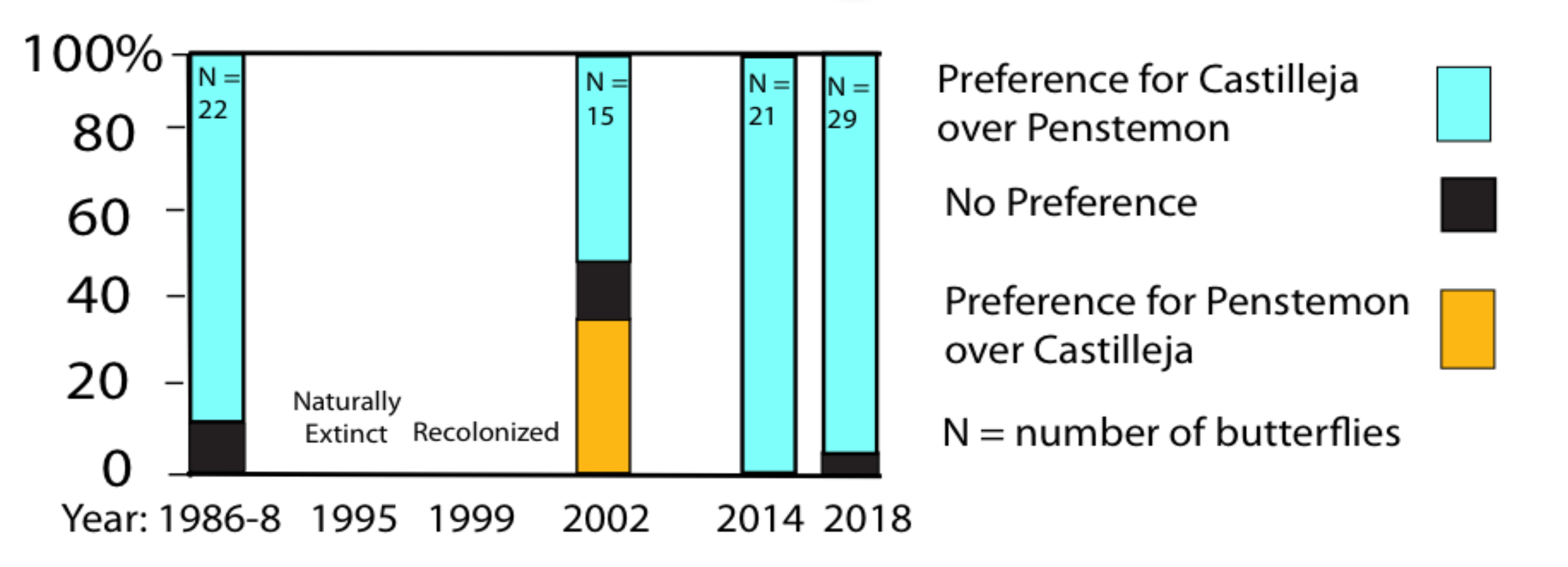
Oviposition preference variation within a rapidly-evolving population was correlated with offspring performance (Singer et al 1988 Evolution)

Preferences diversify after colonizations (Singer & Parmesan 2021 GCB)

This diversification contributes to relationship between population-level diet breadth and range expansion (Lancaster, Nature Eco-Evo 2021)

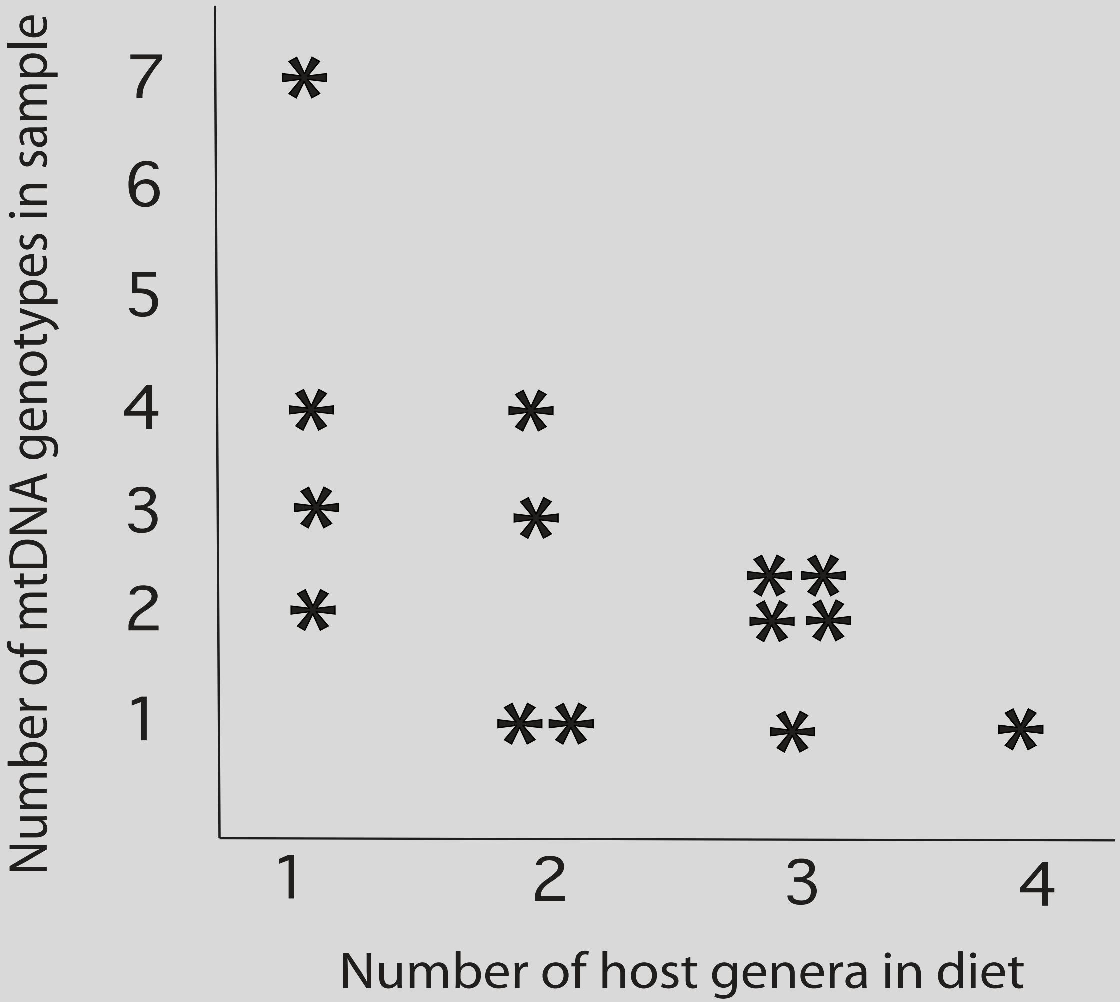
# Changes in diversity of preference rank at Sonora

(Singer & Parmesan 2021 Global Change Biology)



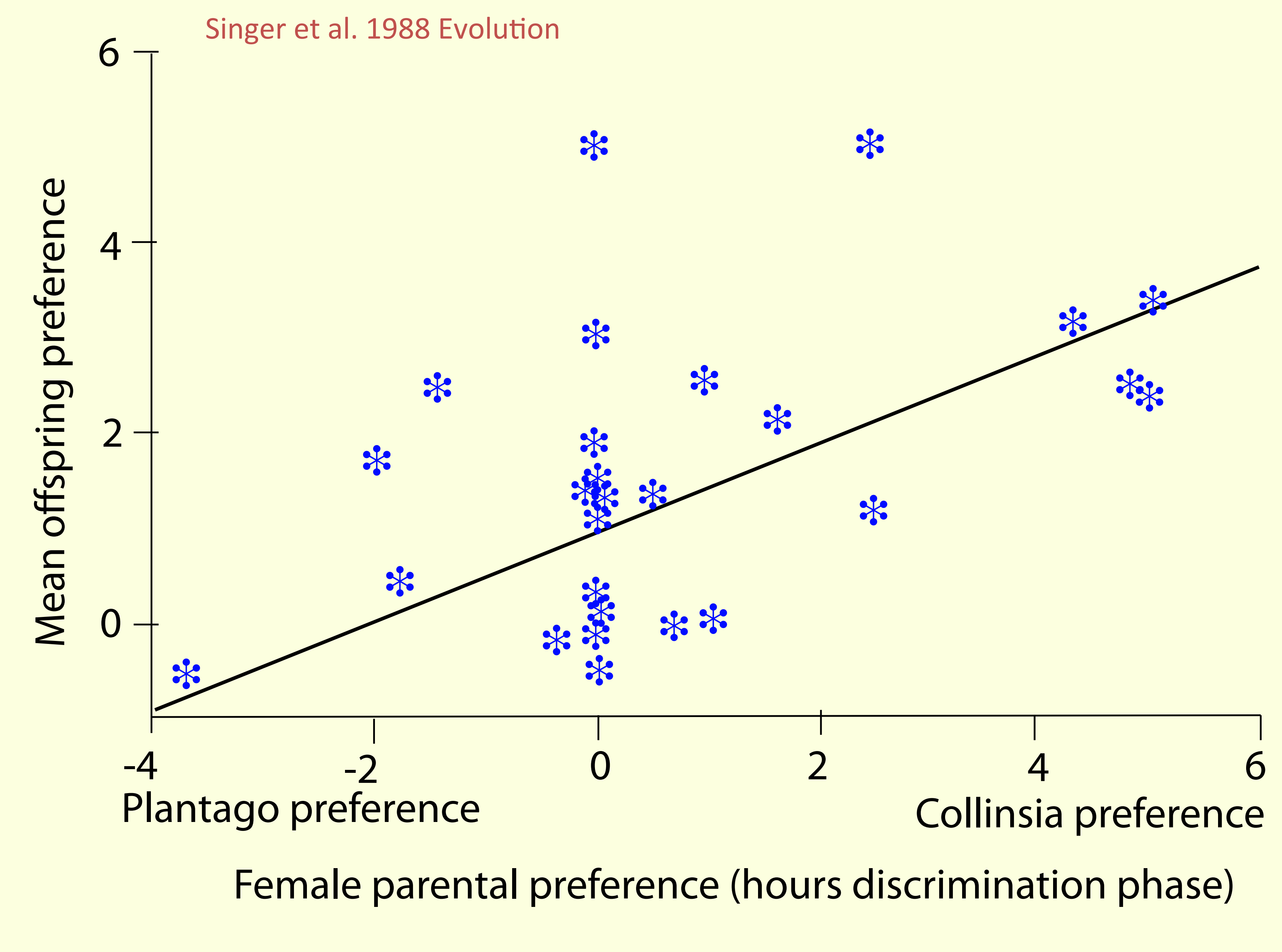
# In the 1980's, number of haplotypes per individual was associated with population-level diet breadth.

Spearman rank test: p = 0.024, two-tailed

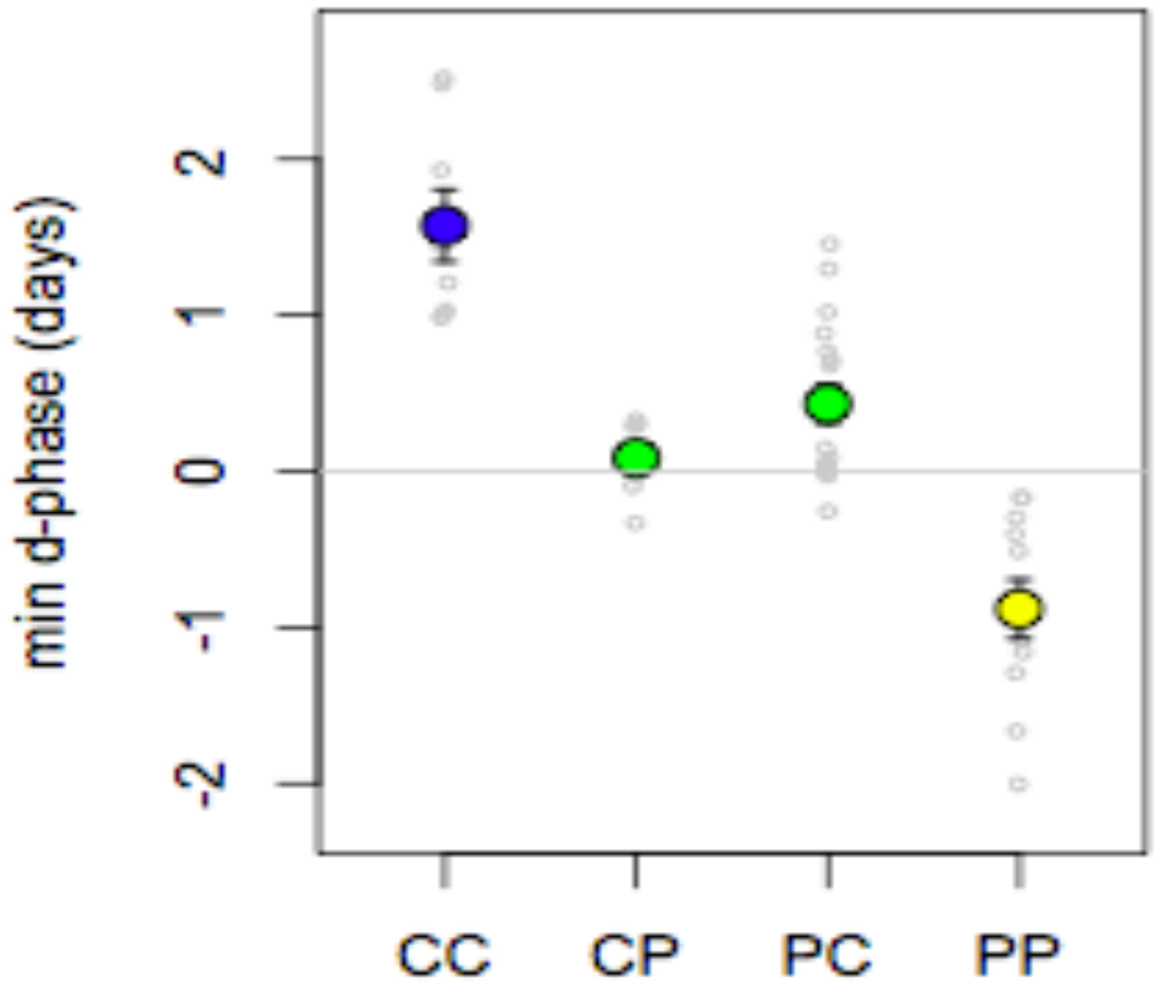


# Perhaps oviposition preference is affected by prior experience as a larva?
# I failed to impress a famous entomologist, Vincent Dethier, at Stanford in 1970

- Dethier: And what do you do, young man?
- Mike: I've been examining how Paul's butterfly uses different hosts at different sites, and I'm beginning to think that there's genetic variation among populations in oviposition preference.
- Dethier: Young man, you really should start by reading the literature. The adults learn to prefer what they ate as larvae. It's called Hopkins' host-selection principle.
- Mike: Oh, not in this case, I think. . . (but he was gone).




**Preference is highly heritable**




Oviposition Preference for *Collinsia* versus *Pedicularis*

Positive values: Prefer *Collinsia*

Negative values: Prefer *Pedicularis*

McBride & Singer
PLoS Biology 2010

# Second chance to impress Vincent Dethier, in Austin, Texas

- Dethier: And what do you do, young man?
- Mike: I'm sure you don't remember this, but ten years ago I was beginning to suspect that the geographical mosaic of diet in *Euphydryas* butterflies involved genetic variation of oviposition preference.Well, now I can prove it!
- Dethier: Everybody knows that! Christer Wiklund's work shows that clearly (and he walked away)

# Insect host preference: its definition, correlates and evolutionary dimensionality

It's multi-dimensional! Example: At Rabbit Meadow in the 1980s a host shift was in progress from *Pedicularis* to *Collinsia*

I already showed you that butterflies varied in discrimination among *Pedicularis.* Non-discriminators were more accepting of the novel host, *Collinsia,* suggesting that when insects add a host they risked losing adaptive discrimination within the traditional host. A good reason for evolved specialization!

# **Insect host preference: its definition, correlates and evolutionary dimensionality**

But NO!!! The ancestral condition had much less acceptance of *Collinsia* but identical frequency of discrimination within *Pedicularis*. And the trend for association between the two preferences was opposite direction from Rabbit Meadow.

The association between the two axes of preference, within and between host species, had evolved significantly in less than 20 generations.

*Annual Review of Entomology*

# Preference Provides a Plethora of Problems (Don't Panic)

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Annual Reviews of Entomology 66: 1-22 (2021)

# The roles of host and habitat preference in Conservation planning: a current example

Climate Change is bringing previously-isolated species and subspecies into contact and causing hybridizations

(Parmesan et al 2022 IPCC WGII Ch 2: terrestrial and freshwater ecosystems)

This phenomen is most widespread in the Arctic but is also predicted to affect Edith's Checkerspot in California, where two endangered subspecies risk hybridizing.

With Polar & Grizzly bears it's feasible to shoot the hybrids; with butterflies, maybe not...

Parmesan, Singer, Wee & Mikheyev ,Biological Conservation in review

# Edith's checkerspot butterfly, le damier d'Édith, *Euphydryas editha*.

I started recording geographic variation of diet and oviposition preferences of Edith's Checkerspot in 1968.

Range of Quino Checkerspot predicted to arrive in San Francisco Bay region before 2050. Parmesan et al. 2015

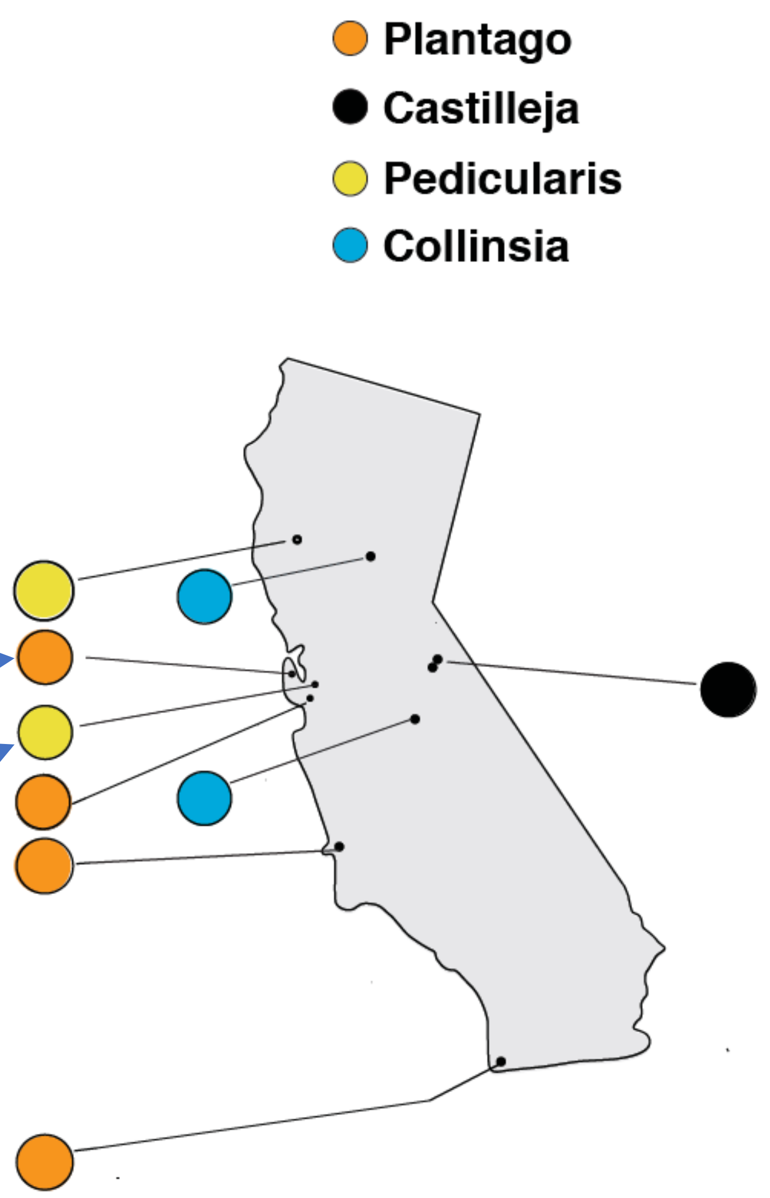
WOODSIDE

Endangered Bay Checkerspot

DEL PUERTO CANYON

OTAY RESERVOIR

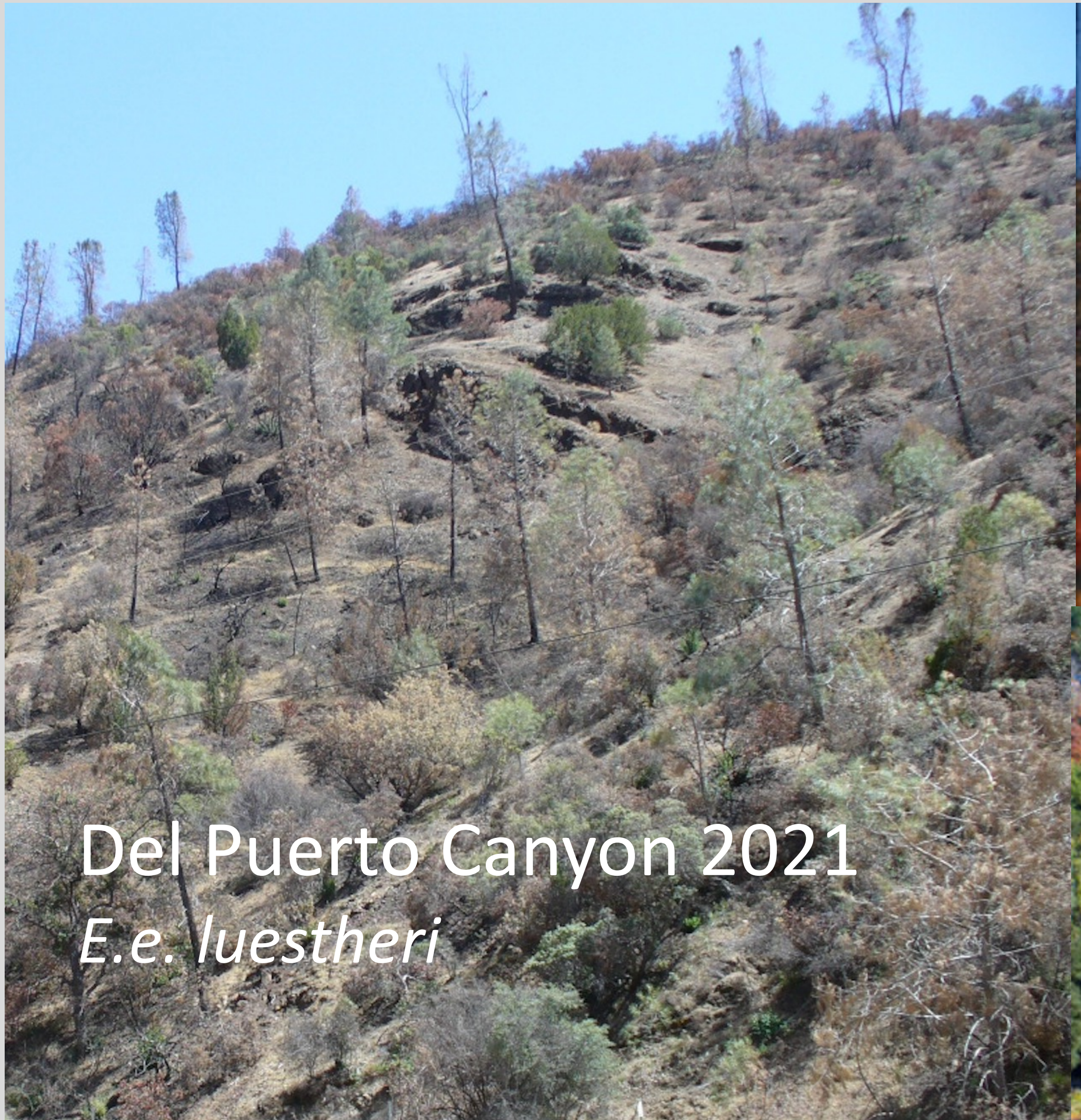
Endangered Quino Checkerspot




GEOGRAPHIC VARIATION OF DIET IN EDITH'S CHECKERSPOT BUTTERFLY

(SINGER, EVOLUTION, 1971)

# Habitats of *Euphydryas editha* and *Homo sapiens*

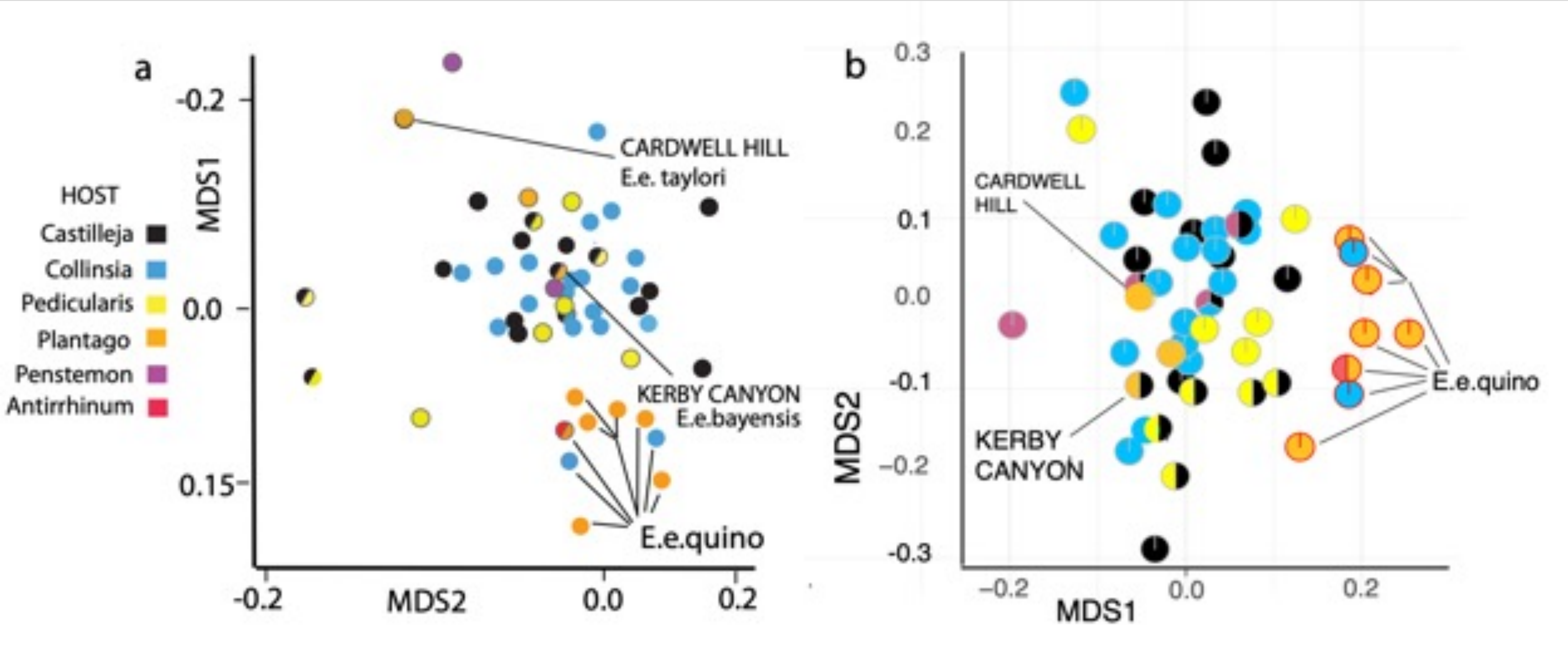


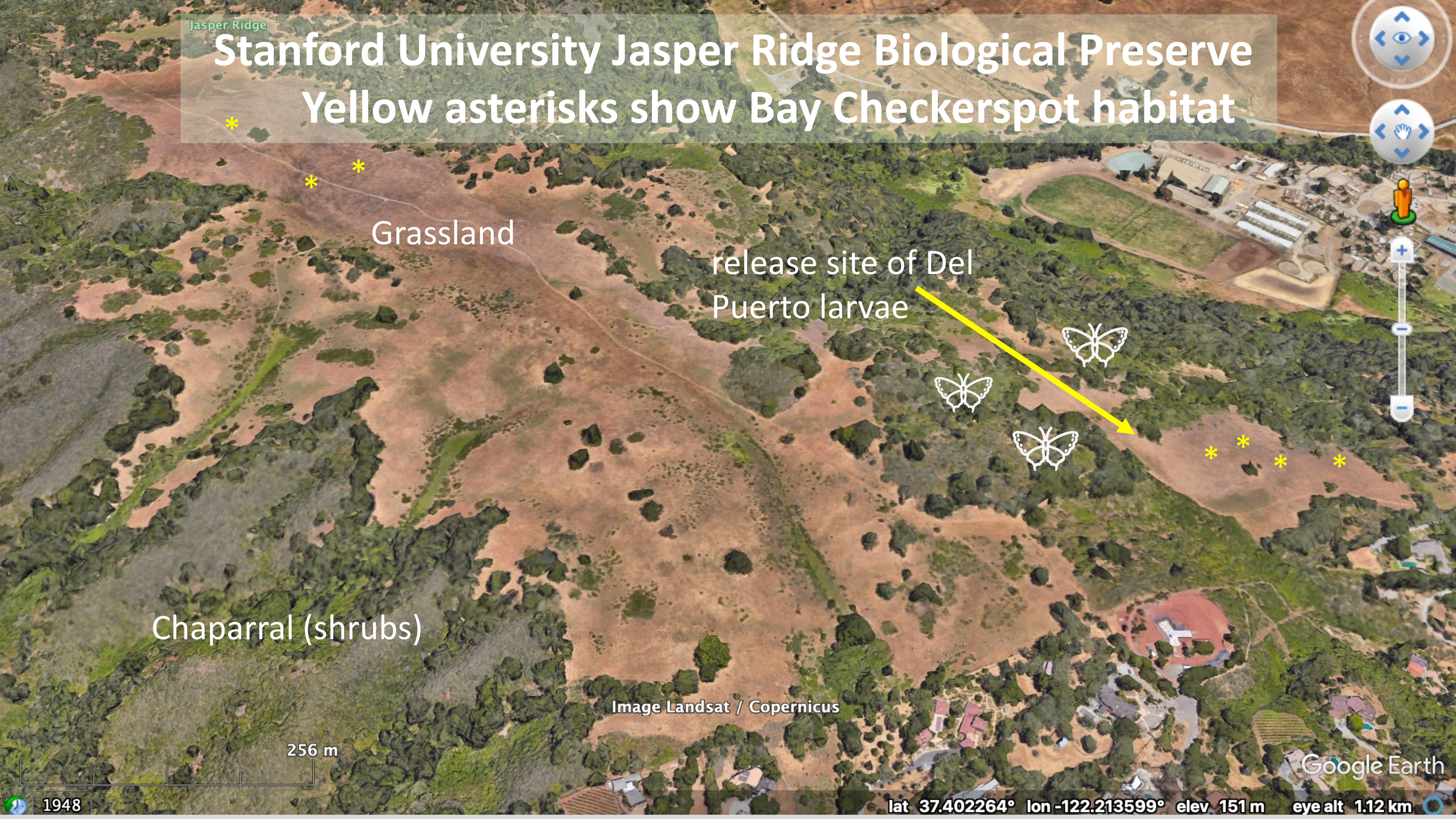


# NMDS plots of *E.editha*, with population diets

Metrics are Fst at left, Jost's D at right. Jost, L., et al.. 2018. Evol. Appl. 11, 1139-

Endangered subspecies: *quino, bayensis, taylori.* (Parmesan, Singer et al in revision)




Jasper Ridge
Stanford University Jasper Ridge Biological Preserve
Yellow asterisks show Bay Checkerspot habitat
Grassland
release site of Del Puerto larvae
Chaparral (shrubs)
Image Landsat / Copernicus
256 m
1948
Google Earth
lat 37.402264° lon -122.213599° elev 151 m eye alt 1.12 km

# Observed evolution of preference: Oviposition preference of *Euphydryas* has sequential components even after habitat choice

1) positive response to visual stimuli = alight and taste with foretarsi

2) positive response to taste is to select height

3) next stage is to seek tactile stimuli and feel with ovipositor

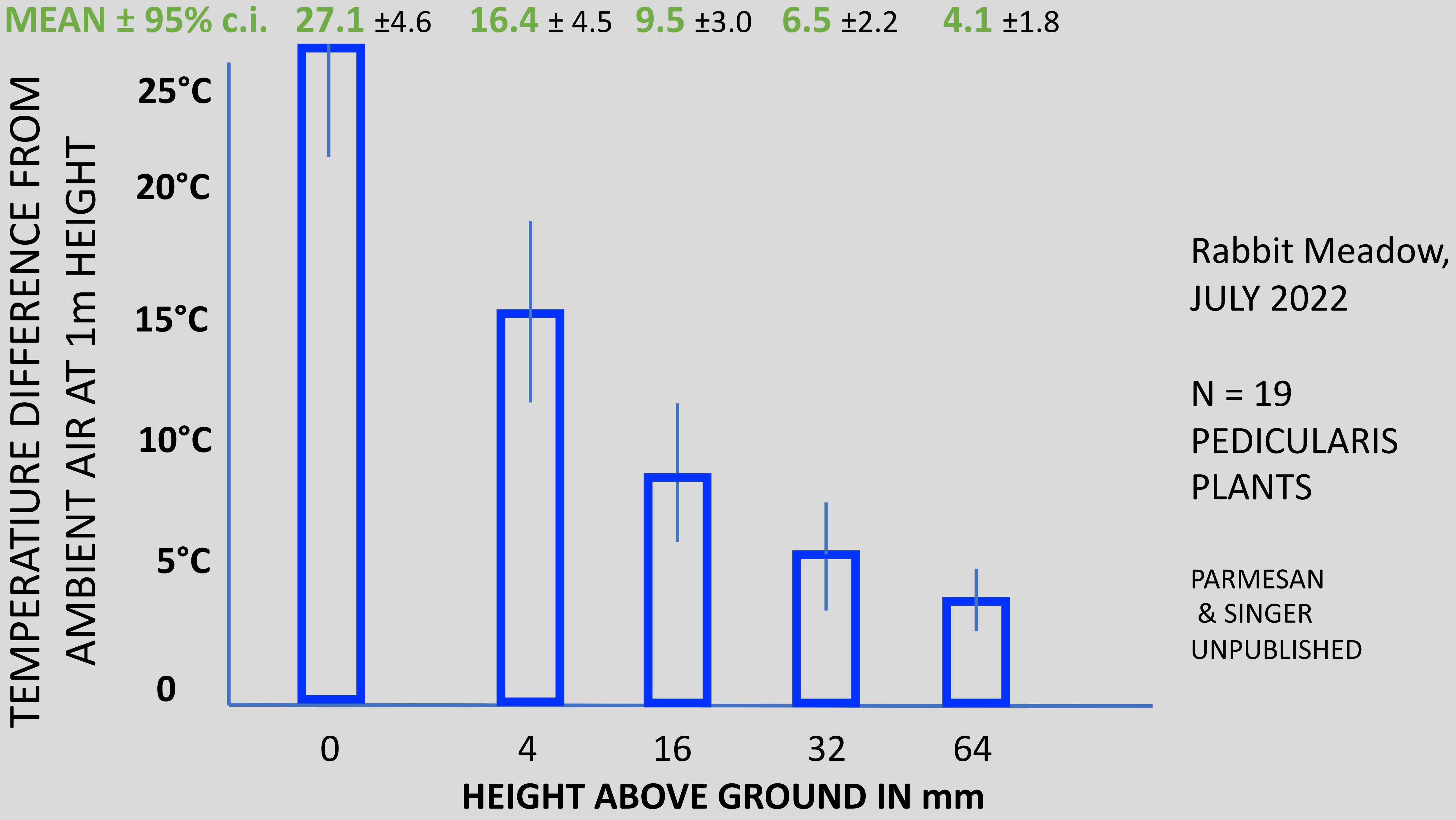
4) positive response to tactile stimuli: lay some eggs!

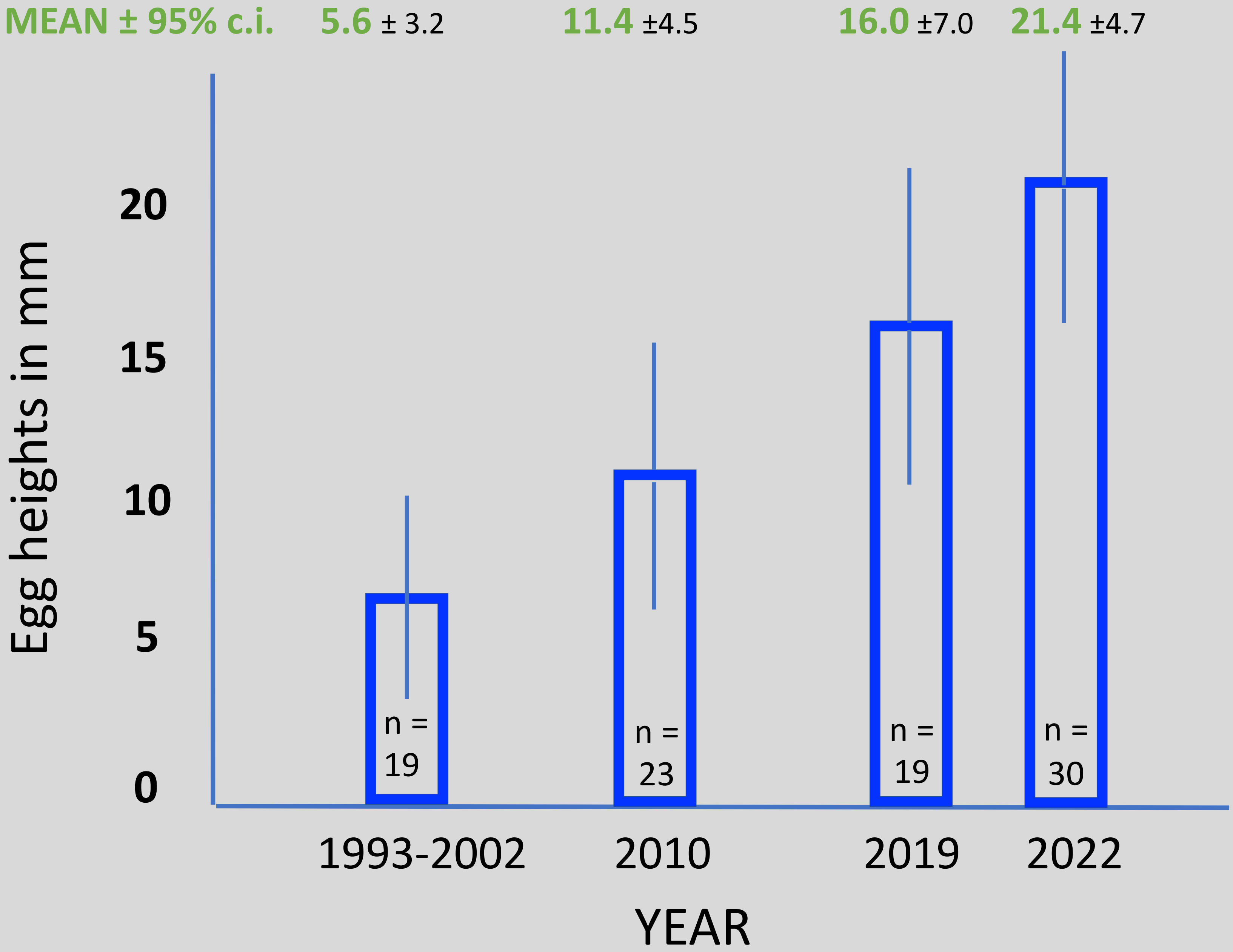
# Rabbit Meadow, Tulare County California, June 2022

3 grazed leaves

eggs

25 July 2019


MEAN ± 95% c.i.
27.1 ±4.6
16.4 ± 4.5
9.5 ±3.0
6.5 ±2.2
4.1 ±1.8
TEMPERATIURE DIFFERENCE FROM AMBIENT AIR AT 1m HEIGHT
25°C
20°C
15°C
10°C
5°C
0
0
4
16
32
64
HEIGHT ABOVE GROUND IN mm
Rabbit Meadow, JULY 2022
N = 19 PEDICULARIS PLANTS
PARMESAN & SINGER UNPUBLISHED



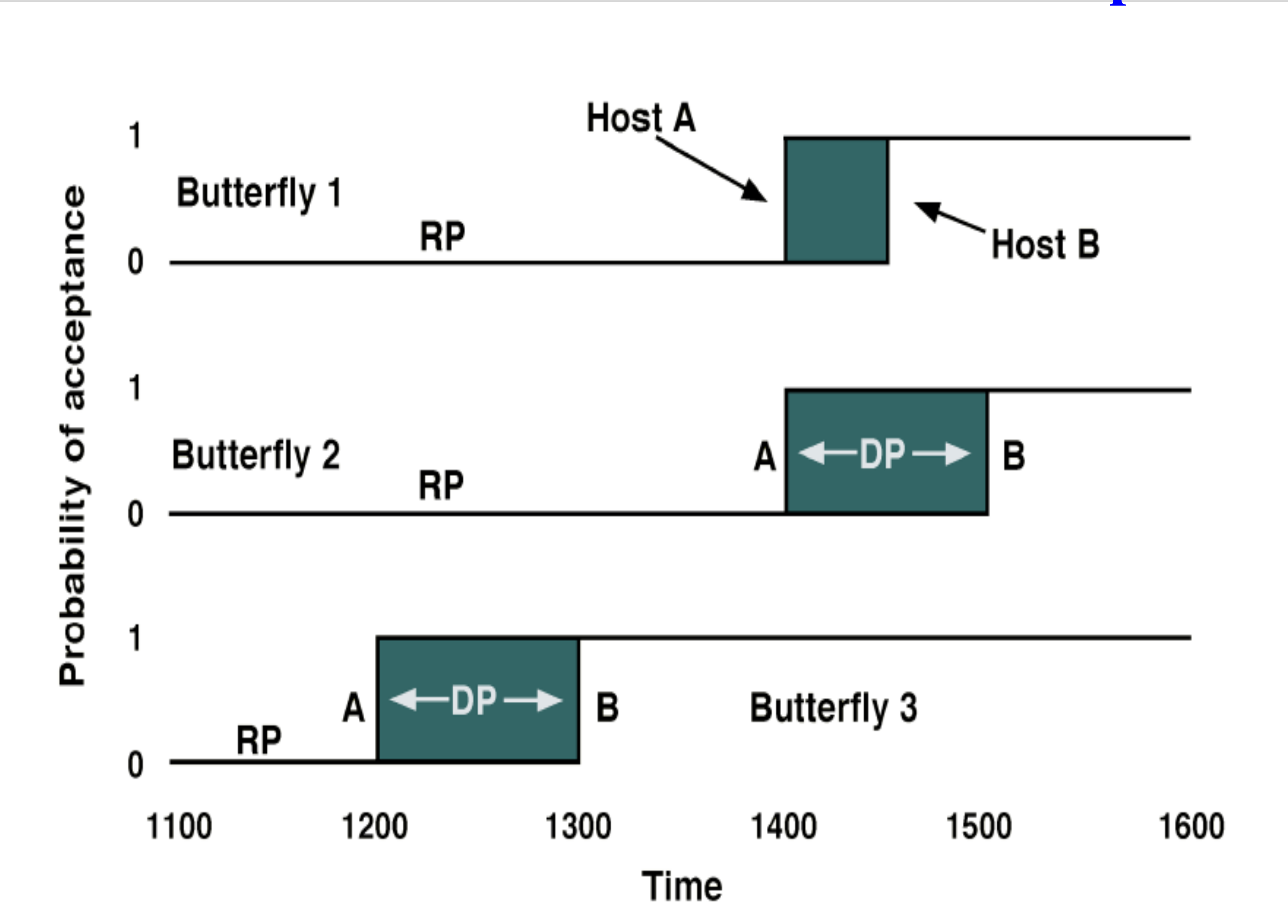

*Euphydryas editha* egg heights at Rabbit Meadow, 1993-2022

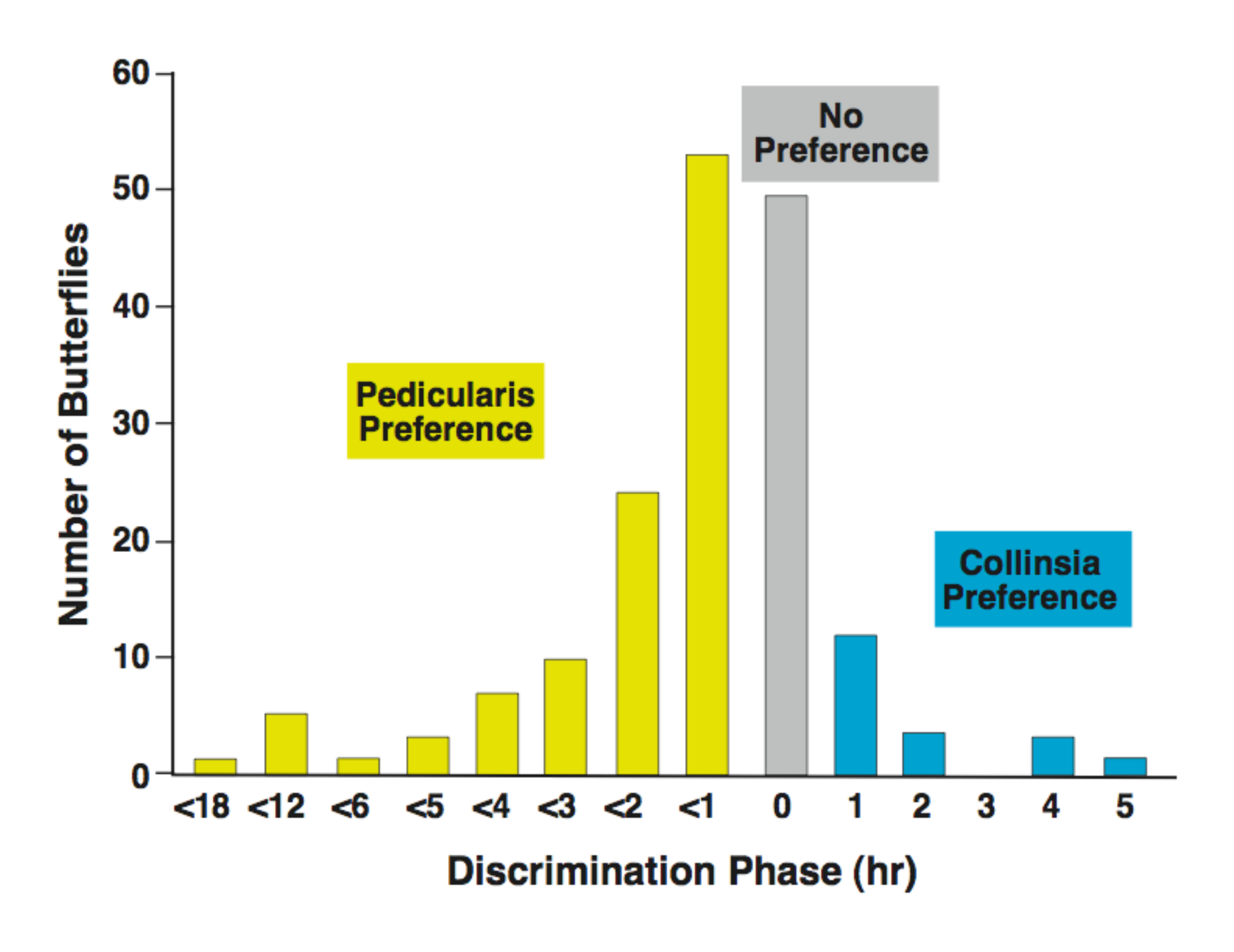
# How to measure oviposition preference for plant chemistry?

# Manipulated oviposition by *E. editha* on *Collinsia*

**Changes over time in host acceptance by three *Euphydryas* butterflies deprived of opportunity to oviposit**

**Butterflies 1 and 2 differ in preference but not motivation; butterflies 2 and 3 differ in motivation but not preference**






- Yellow = preference for *Pedicularis*
- Blue = preference for *Collinsia*

**Distribution of oviposition preferences for 2 host genera at a site where 4 genera were used and diet was evolving**

(Singer 1983 Evolution)

Parmesan Singer

Austin, Texas, April 1983

# Stealin’

Stealin', stealin', pretty mama don't you tell on me.
I'm stealin' back to my same old used to be.

Now put your arms around me like the circle 'round the sun.
I want you to love me mama like my easy rider done.
If you don't believe I love you look what a fool I've been.
If you don't believe I'm sinkin' look what a hole I'm in.

Stealin', stealin', pretty mama don't you tell on me.
I'm stealin' back to my same old used to be.

- Memphis Jug band, Memphis Tennessee, 15 September 1928

- FIN