Table 2. Attractiveness of live and stuffed insect larvae to mosquitoes. Mean number (plus of minus S.E.) of mosquitoes (both sexes) landing in 30 minutes on five larvae on the cage walls.

Species of mosquito	Age (days)	Replicates (No.)	Host	Landings (No.)
Aedes aegypti	19–20	2	Live *Galleria mellonella*	3.5 ± 2.5
			Live *Celerio euphorbiae*	37.0 ± 6.0
Culex tarsalis	27–31	8	Stuffed *Celerio euphorbiae*	6.9 ± 0.8
			Stuffed *Galleria mellonella*	2.4 ± 0.4
Culex tarsalis	27–31	8	Coddled *Celerio euphorbiae*	14.9 ± 0.8
			Stuffed *Celerio euphorbiae*	6.0 ± 0.4
Aedes aegypti	3–13	10	Live *Galleria mellonella*	40.7 ± 2.0
			Coddled *Galleria mellonella*	47.7 ± 0.9

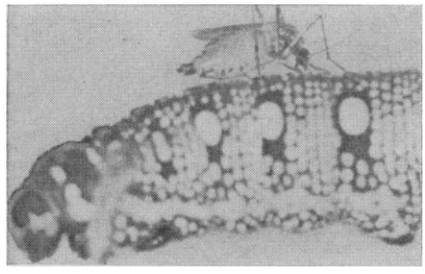

Fig. 1. *Aedes aegypti* engorging on *Celerio euphorbiae* hemolymph.

quitoes did obtain at least partial meals from even intractable living larvae. For example, when *Aedes aegypti* were caged with living *Celerio euphorbiae* that had been injected with 20 μc of P^{32}, many became radioactive, although few obtained noticeably large meals.

Whether these mosquitoes can be expected to feed on insect larvae in nature depends on the extent to which they find the larvae by being attracted to them, rather than by merely encountering them haphazardly, as in a crowded cage. Evidence of attraction for *Aedes aegypti* is (i) the aggregation around a coddled *Celerio euphorbiae* larva, and (ii) the widely different rates of landing on test invertebrates (Table 1). Although no experiments were conducted specifically to identify the attracting stimuli, values in Table 2 offer some indication of their nature. Thus its contrasting color and pattern may have made *Celerio euphorbiae* (alive or stuffed) more attractive than the off-white *Galleria mellonella* (tests 1 and 2). The fact that coddled larvae attracted more mosquitoes than did stuffed ones (test 3) and were at least as attractive as living larvae of the same species (test 4) suggests that heat or a chemical by-product of metabolism may be involved and movement is not. Size of the larva may also play a role. When coddled *Celerio euphorbiae* were exposed four at a time for 1 hour, six, three, one, and zero *Aedes aegypti* fed when the average larval weights were 0.69, 0.16, 0.04 (only 14 mm long), and 0.03 g or less, respectively.

That mosquitoes feed on insects in the laboratory does not prove that they do so in nature. The lack of records of this activity does not conflict with the possibility, because such feedings may well have been overlooked. In serological surveys the gut contents of wild-caught mosquitoes are tested only if dark or red, and then only against vertebrate antiserums. Mosquitoes with pale, swollen abdomens are assumed to have fed on carbohydrate material such as nectar or to have hypertrophy of the fat body, and are not analyzed further. This practice eliminates the possibility of detecting invertebrate meals, which are normally yellow, pale green, or colorless.

In open windswept regions, mosquitoes shelter in clumps of dense vegetation where they are close to feeding larvae; thus the mosquitoes do not necessarily have to cover distances greater than those in our experiments to find larvae. The behavior of *Culex tarsalis*, which did not feed on insects during the first 2 weeks after emergence, suggests that hemolymph may be taken as a last resort if vertebrate hosts are not available. If mosquitoes do indeed feed often on insect larvae in nature, they may be vectors of insect diseases and may even transmit microorganisms from insects to man and other vertebrates.

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Linkage of Lactate Dehydrogenase B and C Loci in Pigeons

Abstract. *Synthesis of lactate dehydrogenase in somatic and gametic tissues of certain avian and mammalian species is controlled by alleles at three loci,* A, B, *and* C. *We report breeding experiments with pigeons that conclusively demonstrate linkage between the* B *and* C *structural loci in this species. The most probable recombination fraction is zero, and contiguity is not excluded. The upper 95 percent probability limit is 4.5 percent. This tight linkage of two loci that produce closely similar polypeptides suggests that the loci acquired their separate identities through a duplication event. Furthermore, the existence of recognizable B- and C-type polypeptides in both the bird and the mammal suggests that the event and the resulting linkage preceded the separation of these fauna. If so, then the linkage has persisted for a very long time.*

Lactate dehydrogenase (LDH) in the somatic tissues of many avian and mammalian species can be resolved into five molecular forms (isozymes) by chromatography and electrophoresis. The isozymes are tetramers formed by association of monomers of two different classes (A and B) in all possible combinations (*1*). Thus, the polypeptide composition of the five isozymes may be designated as follows: LDH-1 (B_4), LDH-2 (A_1B_3), LDH-3 (A_2B_2), LDH-4 (A_3B_1), and LDH-5 (A_4). Studies of electrophoretic variants of LDH in deer mouse (*2*) and in man (*3*) have indicated that the synthesis of the A and B subunits is mediated by alleles at two loci, LDH_A and LDH_B.

Electrophoretically unusual forms of LDH (LDH-X) first appear in testes from certain mammalian and avian species during sexual maturation (*4*). Observations on the pigeon (*5*) have shown that the synthesis of the LDH-X enzyme is dependent on a third genetic locus, LDH_C. In pigeons, therefore, as well as in other species with uniquely testicular forms of LDH, the total complement of LDH isozymes is determined by the activity of alleles at three loci, LDH_A, LDH_B, and LDH_C, each being responsible for the synthesis of a corresponding polypeptide.

A survey of the LDH composition of somatic tissues and testes from approximately 1000 wild pigeons revealed the existence of polymorphisms at both the

Table 1. Results of breeding experiments to determine linkage relationships between LDH_B and LDH_C.

Cage No.	Phenotypes and origins of parents				Distribution of phenotypes among male offspring					
	Male	Origin	Female	Origin	$B^1B^1C^2C^2$	$B^1B^2C^1C^2$	$B^2B^2C^1C^1$	$B^1B^1C^1C^2$	$B^1B^2C^1C^1$	Other
4	$B^1B^2C^1C^2$	Wild	B^1B^2	Wild	3	8	4			0
6b	$B^1B^2C^1C^2$	Cage No. 4	B^1B^2	Cage No. 5		1	1	3	1	0
2b	$B^1B^2C^1C^2$	Cage No. 6b	B^1B^2	Cage No. 4	1	1				0
3a	$B^1B^2C^1C^2$	Wild	B^1B^2	Wild		2	2	3	2	0
5b	$B^1B^2C^1C^2$	Cage No. 3a	B^1B^2	Cage No. 4		3	2			0
8b	$B^1B^2C^1C^2$	Cage No. 4	B^1B^2	Cage No. 3a		1	1			0
8c	$B^1B^2C^1C^2$	Cage No. 8b	B^1B^2	Cage No. 4	1	2	1			0

B and *C* loci (*6*). Consequently, synthesis of LDH isozymes in populations of mature male pigeons can reflect as many as nine different genotypes: B^1C^1/B^1C^1, B^1C^2/B^1C^1, B^1C^2/B^1C^2, B^1C^1/B^2C^1, B^2C^1/B^2C^1, B^2C^1/B^1C^2, B^2C^1/B^2C^2, B^1C^2/B^2B^2, and B^2B^2/B^2C^2. These polymorphisms made it possible to establish matings of appropriate genotypes to determine whether the *B* and *C* loci are linked.

We used wild park pigeons trapped at a single site in Baltimore, Maryland. Previous studies had shown that the frequencies of B^1 and B^2 in this population were 0.97 and 0.03, and of C^1 and C^2, 0.87 and 0.13, respectively (*6*). Phenotypes of the males were determined by electrophoresis of hemolyzates and homogenates of testicular biopsies. Doubly heterozygous males ($B^1B^2C^1C^2$) were selected for the breeding experiments. The *C* locus never becomes active in the female so that the *C* genotype cannot be directly determined. For this reason, females heterozygous at the *B* locus were selected for the matings, with the expectation that approximately 25 percent would be genetically C^1C^2. Methods for preparation and electrophoresis of tissue homogenates and localization of LDH isozymes in starch gel were similar to those described (*4*).

The distribution of phenotypes in the male offspring of matings listed in Table 1 can best be explained by nonindependence of the segregations at the *B* and *C* loci. In the case of cage No. 4, for example, where the phenotypes of the offspring show that the female parent is genotypically $B^1B^2C^1C^2$, one would have expected to find nine different phenotype classes if the loci were segregating independently. In fact, only three male phenotype classes were represented ($B^1B^1C^2C^2$, $B^1B^2C^1C^2$, and $B^2B^2C^1C^1$). The simplest explanation of this finding is a close linkage of the *B* and *C* loci. On the basis of such a linkage, the coupling phase can be deduced to be B^1C^2/B^2C^1 in both parents. Each of the seven doubly homozygous offspring (three being $B^1B^1C^2C^2$ and four being $B^2B^2C^1C^1$) must then have received a nonrecombinant gamete from each parent. The mating thus contributes at least 14 nonrecombinants and 0 recombinants. The eight doubly heterozygous offspring ($B^1B^2C^1C^2$) cannot be so neatly scored.

Observations on this one mating are sufficiently informative to establish linkage between the *B* and *C* loci, and the relation is unequivocably substantiated by the other matings, many of which involved offspring from cage No. 4. Since these other matings are less directly interpretable, a computer program was used to find limits for the recombination fraction.

One cannot readily determine the genotype at the *C* locus in a wild female bird, so initial chances for each of her three possible genotypes were assigned from population frequencies. The likelihood of each pedigree was calculated for a range of possible recombination fractions (*7*). The birds in cages 4, 2b, 5b, 6b, and 8c were treated as from one pedigree of three generations and those in cages 3a and 8b as from another pedigree. The likelihood of the data at a recombination fraction of 0, 10, and 20 percent is, respectively, 1.5×10^{12}, 2.5×10^{9}, and 2.5×10^{6} times greater than at 50 percent (the recombination fraction expected in the absence of linkage). By making the approximation that, initially, all recombination fractions between 0 and ½ are equally likely, the graph of likelihoods (Fig. 1) can be directly interpreted as a graph of the relative probability against the recombination fraction (*8*). The 95 percent probability limits of the recombination fraction are 0 and 4.5 percent (if the loci are on the same chromosome, as seems indisputable), since 95 percent of the area under the graph lies between these values. The extensiveness of the data renders these limits insensitive to the exact form of the prior distribution of recombination fractions. Only a trivial narrowing of the limits ensues, for instance, from the use of a prior distribution based on relative chromosomal lengths (*9*). The results are closely similar to those that would have emerged from an experiment yielding 66 directly countable nonrecombinant gametes and 0 recombinant ones.

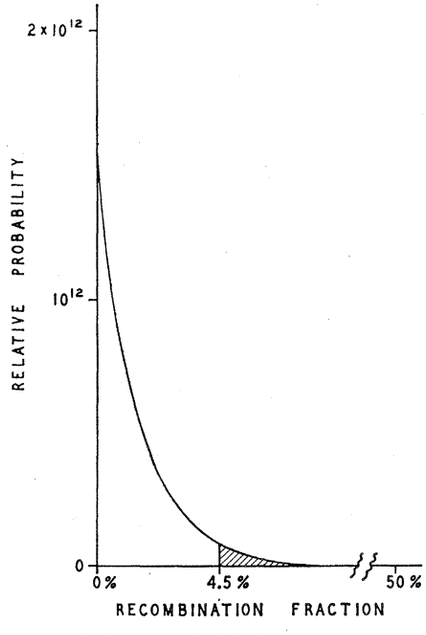

Fig. 1. Relative probabilities plotted against the recombination fractions for the LDH_B:LDH_C interval. The highest probability is that for zero recombination. The unshaded area represents 95 percent of the probability and its upper limit is at a recombination fraction of 4.5 percent.

Many of the catalytic and physicochemical properties of LDH-X are unique (*10*). Even so, subunits (C) of LDH-X reassociate with the B (and with the A) monomers of the other LDH isozymes to form active enzyme molecules (*11*). This evidence points to similarity of the B and C polypeptides of LDH. In the pigeon, the *B* and *C* structural loci are closely linked, as

shown above, and contiguity is not excluded. Such linkage of two loci coding for similar polypeptides suggests that one may have arisen from the other or that they both stem from a common origin.

The fact that *B* and *C* polypeptides occur homologously in birds and in mammals suggests that the *B* and *C* loci had separate identities before the evolutionary separation of birds and mammals. If their separate identities are assumed to have originated by tandem duplication, these loci have thus remained closely linked for a long period of time, at least in birds.

Despite the close linkage, there is a wide difference in the biological behavior of the two loci. The activity of the *B* locus is manifest in both sexes and in all tissues throughout life, whereas the activity of the *C* locus is restricted to a particular sex, a particular tissue, and a particular stage of maturation. Thus, as is frequently the case in microorganisms, the control mechanisms involved may be specific to a short DNA segment constituting one or more loci. The linkage indicates that they are certainly not whole-chromosome mechanisms of the type occurring, for example, in normal "X-inactivation."

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Carbon Dioxide Compensation Points in Related Plant Species

Abstract. *Both high and low CO_2 compensation concentrations were found in the plant genera*—Panicum, Cyperus, *and* Euphorbia. *Within each genus, however, high and low compensations were found in different subgenera. Thus, they may not be genetically closely related. No significant differences in CO_2 compensation were found among 100 genetic lines of* Triticum aestivum *L. or among 20 lines of* Hordeum vulgare *L.*

The atmospheric concentration of CO_2 at which respiratory release of CO_2 within illuminated leaves is in balance with photosynthetic CO_2 fixation —the CO_2 compensation point—differs markedly among plant species (*1*). Species that have a CO_2 compensation point near zero part per million (ppm) have rates of photosynthesis in intense light and ambient air nearly twice as great as species with compensation points of 50 ppm or greater.

Species with low CO_2 compensation points apparently lack photorespiration (*2*), their net photosynthesis is not suppressed by O_2 (*3*), and they fix CO_2 by carboxylation of phosphoenolpyruvate (a 4-carbon pathway) (*4*). They are also characterized by having vascular bundle sheath cells containing specialized chloroplasts which appear to be particularly active in starch formation (*5*). Whether all these traits are necessarily related to high potential for photosynthesis has not been determined, nor has the genetic control of any of these processes been studied, because no significant genetic variability has been found for these traits within a species or within closely related species from which viable crosses could be obtained.

Compensation measurements were made in a closed system consisting of a test tube (2 by 15 cm) connected in series by glass tubing to an air pump, a desiccant column, and an infrared gas analyzer. A leaf, or a small branch in the case of small-leaved dicotyledonous species, was excised beneath air-free water. Air-free water (5 ml) was placed in the test tube, and the leaf or branch inserted into the tube with its base in the water. The test tube was connected to the system, immersed in a water bath which controlled leaf temperature at 23° ± 1°C, and illuminated through an additional 8-cm water filter by four 150-watt reflector spot lamps mounted 50 cm from the leaf. Photosynthesis in the leaves removed the CO_2 from the system until the CO_2 compensation concentration was reached. This required about 15 min-

Table 1. Occurrence of high and low CO_2 compensation points among species of *Euphorbia*, *Panicum*, and *Cyperus*.

Species with compensation point	
< 10 ppm	> 50 ppm
Euphorbia	
Subgenus Chamaesyce Raf.	Subgenus Agloma (Raf.) House
Euphorbia glyptosperma Engelm.	*Euphorbia corollata* L.
E. maculata L.	*E. hexagona* Nutt.
E. missurica Raf.	*E. marginata* Pursh.
E. serpyllifolia Pers.	Subgenus Poinsettia (Graham) House
E. supina Raf.	*E. dentata* Michx.
	E. heterophylla L.
Panicum	
Subgenus Eupanicum Godr.	Subgenus Dischanthelium Hitchc. & Chase
Panicum anceps Michx.	*P. maximum* L.	*Panicum oligosanthes* Schult.
P. antidotale Retz.	*P. miliaceum* L.	*P. praecocius* Hitchc. & Chase
P. capillare L.	*P. minus* Nash.	Subgenus unknown*
P. coloratum Walt.	*P. obtusum* H. B. K.	*P. bisculatum* Thumb.
P. dichotomiflorum Michx.	*P. plenum* Hitchc.	*P. milioides* Nees ex trin.
P. hallii Vasey	*P. virgatum* L.	
Subgenus unknown*		
P. laevifolium Hack		
P. prolutum F. Muell.		
P. stapfianum Fourc.		
P. turgidum Forsk.		
Cyperus		
Cyperus esculentus L.		*Cypserus papyrus* L.

* Not listed in Hitchcock (*9*).