nations, we can show how simple discriminations combine to determine the rate at which a given matching or symbolic matching discrimination will be learned.

Figure 1 shows the mean percentage of correct responses for each session for all complex discrimination groups and the two simultaneous discrimination groups. The upper abscissa has been used for all discriminations involving colors on the side keys. The lower abscissa has been used for all procedures using lines on the side keys. Because one session on the upper abscissa is equal to 2.5 sessions on the lower abscissa, two sets of data points will coincide if one involving line comparisons takes 2.5 times as long to learn as one involving color comparisons.

The relationship between abscissas was chosen empirically to test the following hypothesis: the relative difficulties of any pair of discriminations (simple or complex) bear the same quantitative relationship to one another if the discriminations of that pair differ from each other only in the sample stimulus dimension or only in the comparison stimulus dimension. For the curves in Fig. 1, one function of each pair was generated by using colors on the side keys. The other member of each pair was obtained by using lines on the side keys. The data support the hypothesis because the functions fall into three distinct pairs. The center-key stimulus determines the degree of separation among the pairs of curves.

The hypothesis stated above may also hold when pairs of discriminations differ only in the sample stimulus dimension. Figure 2 shows the mean percentage of correct responses for each session for all complex discriminations and for the simple successive discrimination procedures. The upper abscissa has been used for all discriminations involving colors on the center key. The lower abscissa has been used for all procedures using line samples. One session on the upper abscissa is equal to 4.5 sessions on the lower abscissa.

Four of the six functions support the hypothesis. Given a pair of discriminations which differ in no other way, the one having line samples takes 4.5 times as long to learn as the one having color samples. However, the curves for color matching and symbolic line matching do not coincide. Indeed, there is no linear transformation which will bring these curves together (*8*).

We have shown that the relative rates of learning for matching and symbolic matching may be accounted for by the discriminability between sample stimuli and between comparison stimuli, with the former playing the more important role. Identity between a sample and one of the comparison stimuli plays no role for pigeons. Put another way, matching-to-sample is just as symbolic as is the symbolic matching problem. In both paradigms, pigeons learn a set of a specific "if . . . then . . ." rules, with the sample stimulus serving an "instructional" function to indicate which of the comparison stimuli is the correct one.

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8. Examination of learning curves for individual subjects in the symbolic line matching group revealed that the failure of the two functions to coincide in Fig. 2 was due, in large part, to one atypical bird. Performance of this bird did not rise above chance until after session 85.
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10. This research was carried out at Columbia University in cooperation with the late W. W. Cumming, and was supported by NIMH grant MH-10384.

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## Sexual Selection in a Wild Population of the Butterfly Danaus chrysippus L.

Abstract. Danaus chrysippus *has two common forms,* chrysippus *and* dorippus, *in east Africa. Form* chrysippus *males have a mating advantage lasting 3 to 4 months, which is lost as their frequency increases. Female* dorippus *are normally superior to female* chrysippus *in sexual vigor. Sexual selection favoring different morphs in each sex contributes to the maintenance of the polymorphism.*

Darwin defined sexual selection as the advantage certain individuals had over others of the same sex and species solely in respect of reproduction. As defined, the phenomenon has been demonstrated frequently in laboratory conditions, for example, between mutants and karyotypes of *Drosophila* species (*1*) and different genotypes in mice (*2*), but its detection in wild populations has remained elusive. Here I present evidence for sexual selection involving both sexes of the polymorphic butterfly *Danaus chrysippus* (Danaidae) in the field.

*Danaus chrysippus* is ubiquitous in

Table 1. Mating success of male *Danaus chrysippus* forms *chrysippus* and *dorippus* between February 1972 and March 1974 at Dar es Salaam, Tanzania. Sample sizes are given in parentheses.

| Period | Frequency of *chrysippus* in | | Frequency of *dorippus* in | |
|---|---|---|---|---|
| | Population | Mating pairs | Population | Mating pairs |
| February–March 1972 | 0.38 (10) | 0.29 (2) | 0.62 (16) | 0.71 (5) |
| April–July 1972 | 0.41 (96) | 0.59* (19) | 0.59 (138) | 0.41* (13) |
| August 1972–March 1973 | 0.17 (78) | 0.17 (13) | 0.83 (385) | 0.83 (65) |
| April–June 1973 | 0.29 (69) | 0.43† (27) | 0.71 (169) | 0.57† (36) |
| July–August 1973 | 0.26 (102) | 0.13* (7) | 0.74 (294) | 0.87* (47) |
| September 1973–March 1974 | 0.17 (91) | 0.14 (17) | 0.83 (458) | 0.86 (103) |

* $P < .05$ from $\chi^2$ tests. † $P < .02$ from $\chi^2$ tests.

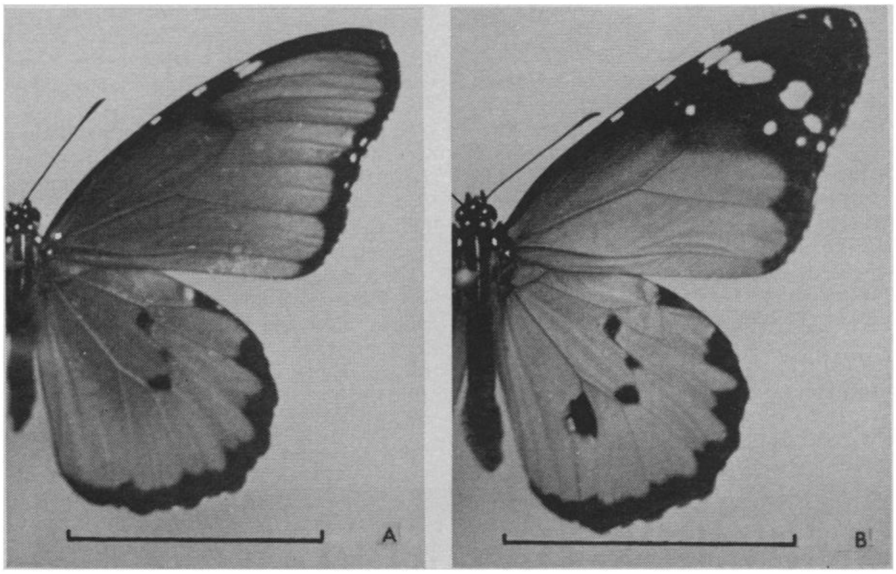

Fig. 1. (A) Female form *dorippus* and (B) male form *chrysippus* of *Danaus chrysippus*. The ground color may be either (A) nut-brown or (B) orange in both forms. Scale bars show natural size of half butterfly.

grassland throughout Africa south of the Sahara Desert. Abundance varies with season, being highest following the two rainy seasons and declining in the intervening dry periods. Over much of its range the species is polymorphic: four color forms occur sympatrically in east Africa (*3*) of which two, *chrysippus* and *dorippus* (Fig. 1), are the subject of this study. Courtship behavior involves a transfer of pheromone from abdominal hair pencils of the male to the antennae of the female as in the tropical American species *Danaus gilippus* (*4*).

The population studied inhabits rough grassland on the campus of the University of Dar es Salaam, Tanzania. I have observed it for 26 months (February 1972 to March 1974), during which 3284 butterflies including 354 mating pairs involving forms *chrysippus* and *dorippus* were examined (*5*). Expected mating frequencies are calculated monthly as both sex and morph ratios vary continuously. They are based on the premise that, in the absence of sexual selection, the proportion of each morph within each sex found pairing is expected to equal its proportion in the population. Deviations from expectation lying in the same direction in adjacent months or over longer periods are amalgamated, and $\chi^2$ is calculated. Frequencies in the population and in mating pairs are shown in Table 1 for males.

At the start of the study neither type of male showed any mating advantage. From April to July 1972, *chrysippus* males had a significant advantage (*6*), while from August 1972 to March 1973 no advantage to either form was apparent. The 1973–1974 cycle began in April to June 1973 with *chrysippus* males again showing superior sexual vigor. In July and August, the advantage switched briefly to *dorippus* males, and this was followed by a long period (September 1973 to March 1974) of selective neutrality.

During and for a short period after the long rains (April and May), the superior sexual vigor of *chrysippus* males must contribute to the rapid increase in the frequency of this form (from 32.1 to 51.7 percent in March to June 1972 and 10.4 to 31.8 percent in March to June 1973), which coincides with a period of fast population growth. That this advantage is lost (1972) or reversed (1973) when the frequency of form *chrysippus* reaches its annual peak suggests the operation of frequency-dependent selection in which a form is favored when rare and selected against when common. However, density-dependent selection is an alternative hypothesis, as population density is maximal at approximately the same time. Climatic selection can probably be ruled out as a factor in mate selection because *chrysippus* males continue to enjoy a mating advantage in June (and July 1972), when it is usually dry. Form *dorippus* has a strong selective advantage in dry periods, when its frequency increases, but apart from July and August 1973, this is apparently not the result of sexual selection favoring the males.

Female *dorippus* had a mating advantage over the whole investigation period, except in December 1972 when form *chrysippus* females had an advantage ($\chi^2_{(1)} = 4.086$; $P < .05$). Deviations from expectation are negative for *chrysippus* females found pairing in 21 of the 25 remaining months; which is highly significant ($\chi^2_{(1)} = 11.56$; $P < .001$). Therefore, from April to June or July, sexual selection favors different forms in the two sexes. The result of selection for *chrysippus* males and *dorippus* females may be an excess of unlike pairings (*7*) leading to a high proportion of heterozygotes. After one round of disassortative mating, many matings will give a backcross segregation (1 : 1), thereby triggering an increase of the genetically recessive *chrysippus* form. In dry periods, the superior sexual vigor of *dorippus* females could alone account for the increasing frequency of this form.

As there is evidence for nonrandom mating in the same population (*7*), the detection of sexual selection in both sexes in addition suggests a behavioral regulatory mechanism capable of achieving rapid change in the equilibrium point of a balanced polymorphism in response to seasonal or density effects. The superior sexual vigor of *chrysippus* males for a period of 3 to 4 months each year, and of *dorippus* females over the whole year (with occasional exceptions), must help to maintain the polymorphism. The manner in which mating behavior is regulated is not known, but it is probable that the relative frequencies of the two types of male play an important role. Sexual recognition may be based on either the contrasting color patterns, the production of different pheromones by males of the two forms, or a combination of both (*8*).

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