emerge from the interaction of changing behavior and increasing numbers of ants.

It is important to recognize that foraging strategy derives from an interaction between colony size and the recruitment behavior of individuals. A single recruitment behavior may not lead to the same foraging strategy in different colonies, or in a single colony over a period of time. All of these features are products of the way information is exchanged in the system. Many of the patterns of foraging we observe for an ant colony may be determined by the nature of the information exchange and its inherent limitations.

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Two Critical Day Lengths for the Determination of Wing Forms and the Induction of Adult Diapause in the Water Strider, *Aquarius paludum*

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Wing dimorphism is widespread among insects [1,2]. In some species showing wing dimorphism, there are seasonal variations in wing forms: The adults of the summer generation are predominantly short-winged or wingless, and those of the autumn generation are long-winged [2]. This wing polyphenism can be linked to the seasonal variation in habitat. The short-winged or wingless insects reproduce in habitats with sufficient food, and no migration occurs during favorable seasons, whereas the long-winged insects migrate for the overwintering sites before stressful periods [3]. Seasonal variations in wing dimorphism have been shown in some water striders

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(Heteroptera: Gerridae) living in Europe and North America, including *Aquarius paludum* [4–6]. These studies have been made exclusively on bivoltine populations and showed a specific link between wing form and reproductive status. The adults of the first generation are mostly short-winged or wingless and promptly begin to reproduce, and the adults of the second generation are mostly long-winged and enter diapause. Vepsäläinen showed in one of these water striders, *Gerris odontogaster*, that increasing photophase in the nymphal stage induces micropterous forms and prompt reproduction in the summer generation, whereas decreasing photophase results in macropterous forms and adult diapause in the second generation [7, 8]. He stated that the mechanism determining wing forms is the same as the mechanism controlling diapause [7].

In Kochi, Japan (33° 30'N, 133° 35'E), however, *A. paludum* shows trivoltinism [9]. The proportion of macropterous adults was 40.0 and 93.7% in the samples of the first and the second generations, respectively [10]. We collected the fifth instar nymphs of the third generation from a waterway in Kochi in mid-October, 1991; 94.1% of emerging adults were macropterous (*n* = 34). Thus, brachypterous adults are higher in proportion only in the first generation, and the specific link between wing form and reproduction does not appear in the second generation. How do environmental factors produce such unique phenology in *A. paludum*?

First, we examined the effect of stationary photoperiod on the wing form and diapause in this species. First instar nymphs from macropterous parents were reared under different constant photoperiods during nymphal and adult stages at 20 ± 2 °C by the methods previously reported [10]. The females that did not lay eggs for 30 days after adult emergence were judged as being in diapause, because all females not in diapause began to lay eggs within 30 days after adult emergence.

Constant long-day conditions induced the brachypterous form and reproduction, whereas constant short-day conditions caused the macropterous form and
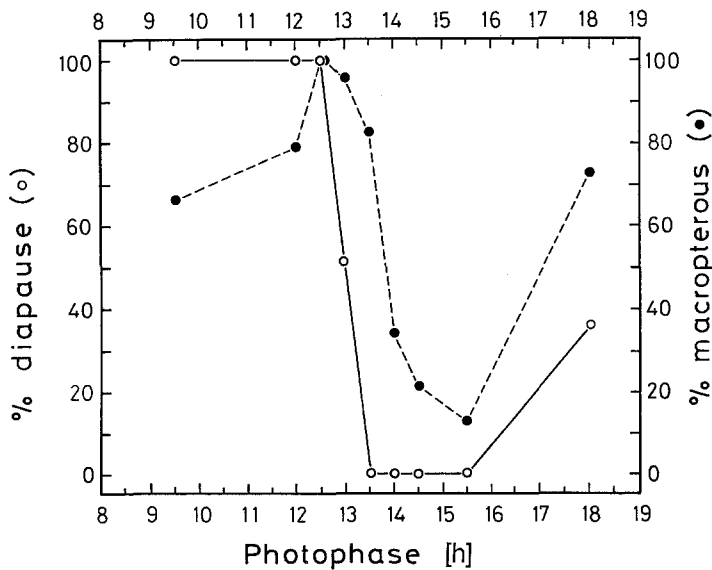
Fig. 1. Photoperiodic response curves for the determination of wing forms and the induction of adult diapause in *Aquarius paludum* at 20 °C; *n* = 30–117 for wing form, *n* = 14–54 for diapause
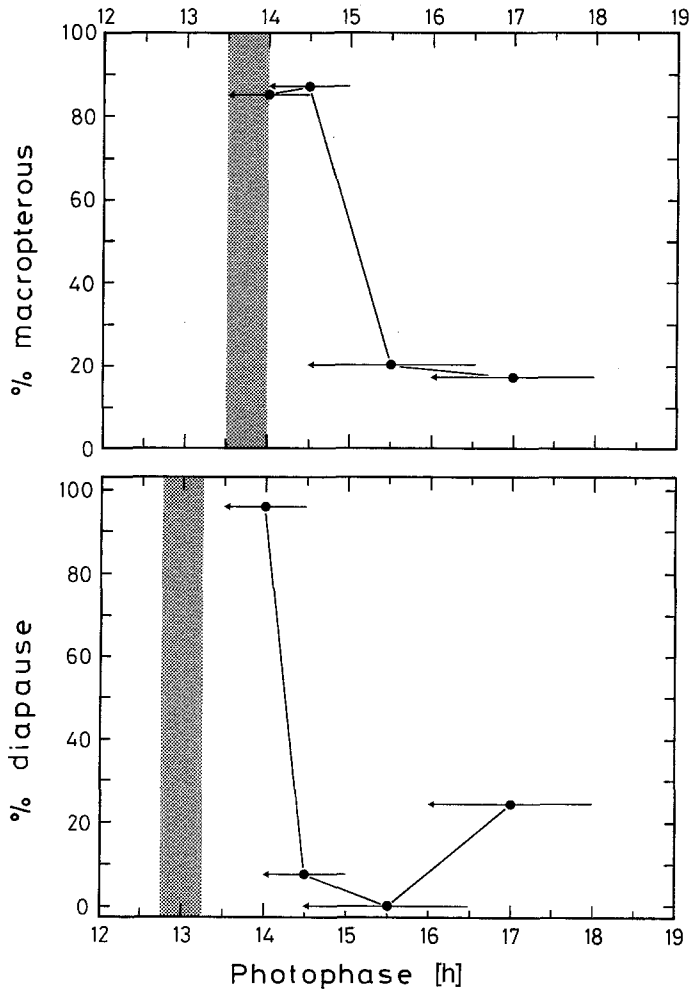

Fig. 2. Effect of decreasing photophase on the determination of wing forms and the induction of adult diapause in *Aquarius paludum* at 20 °C. *Shaded zones* show the critical day lengths defined by stationary photoperiods, *arrows* the range over which photophase was changed; *n* = 31–96 for wing form, *n* = 14–40 for diapause

diapause (Fig. 1). The critical day length for the determination of wing forms was, however, longer by about 45 min than that for the induction of adult diapause. We then examined the effect of decreasing photophase on wing form and diapause. First instar nymphs from macropterous parents were reared under stepwise decreasing photophases during the nymphal stage at 20 ± 2 °C. The photophase was decreased stepwise by 15 min every 3 or 5 days during the first to the fourth (penultimate) nymphal instars. Under stepwise decreasing photophase, the critical day lengths shifted to longer values by about 1 h in both responses independently (Fig. 2). Responses to decreasing photophase have been reported even in some insects with a distinct critical day length defined by stationary photoperiods. A decrease within the long-day range has a short-day effect (e.g., [11–13]). *A. paludum* also responded to a decrease in photophase, but only within a range of about 1 h, close to each critical day length determined by stationary photoperiods (Fig. 2), like a moth, *Loxostege sticticalis* [13].

In *A. paludum*, the nymphs of the first generation develop in May and early June when the natural day length is longer than either of the two critical day lengths for wing form and reproduction (Fig. 3). The majority become brachypterous adults and promptly begin to reproduce. The nymphs of the third generation develop in late September and October when the natural day length is shorter than the two critical day lengths if the effect of decreasing photophase is considered (Figs. 2, 3). Most of them become macropterous adults and enter diapause.

Because the first instar nymphs hatching in July are killed by high temperature and solar radiation and so never reach adulthood [9], the nymphs of the second generation develop in August and early September when the natural day length is between the two critical day lengths for wing form and diapause if the effect of decreasing photophase is considered (Fig. 3). Therefore, most of them become macropterous adults and promptly begin to reproduce. Thus, this unusual combination of wing form and reproductive status in the second generation of *A. paludum* is achieved by the exposure to photophases between the two critical day lengths for wing form and diapause.
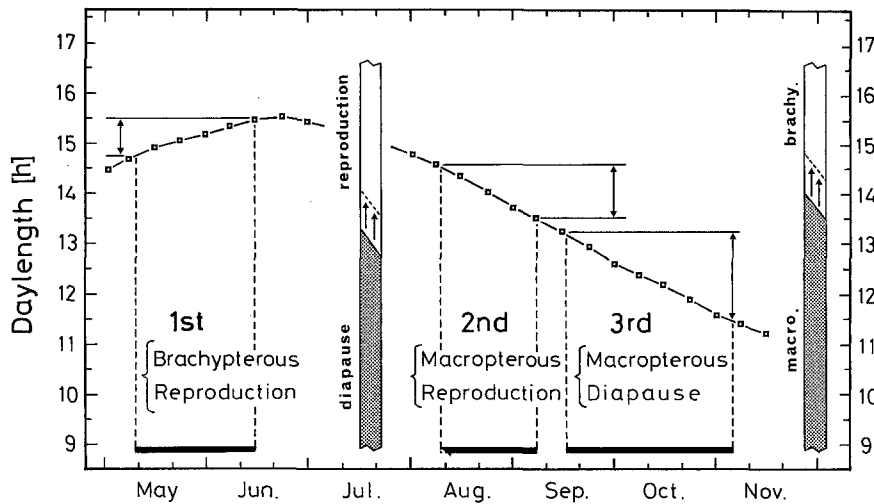
Fig. 3. Schematic representation of the life cycle of *Aquarius paludum* in Kochi, Japan, and the leading role of photoperiod. The *horizontal bars* in the lower position show the nymphal period of the three generations. Natural day length including civil twilight at 35 °N is shown after [18]

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The ecological significance of the macropterous form in the second generation in *A. paludum* is apparently the ability to migrate before reproduction because water surface habitats increase in September [10]. Here, we emphasize again the advantage of migration in this generation, leaving many overwintering offspring: (1) In September, the mortality during migration seems much lower than in summer because the lower solar radiation at this time does not induce lethal high temperatures and desiccation. (2) Heavy rainfall in September produces many new habitats for *A. paludum*, which will not immediately dry up because temperatures become lower after September. (3) Competitive *Aquarius elongates* and *Gerris latiabdominis* migrate in August or September to overwintering sites on land [14, 15].

In many insects, photoperiod controls both morphological polyphenism and a diapause shown in the same developmental stage [7, 8, 16, 17]. In most cases, the critical day length was shown to be common between the two responses [16]. In larvae of an univoltine butterfly, *Sasakia charonda*, however, the critical day length for the induction of the morphological diapause form is slightly longer than that for the induction of physiological diapause. Therefore, under natural conditions, diapause-form larvae appear earlier in the season than diapause larvae [17].

Here, we show that there are two different critical day lengths for morphological polyphenism and diapause in *A. paludum* and that this species responds to a decrease in photophase within near-critical zones. As a result of these responses, the second generation of *A. paludum* develops between the two critical day lengths in Kochi. We suggest that the physiological mechanism for photoperiodic response in insects can evolve different critical day lengths for morphological and physiological polyphenism if there is an ecological demand.

BUCHBESPRECHUNGEN

Biologie der Spinnen. Von R. F. Foelix. Stuttgart-New York: Thieme 1992. 331 S., 201 Abb., 6 Tab., DM 48,–.
Der „Foelix" ist ein Nachschlagewerk für viele Aspekte der Biologie der Spinnen, das längst seinen festen Platz hatte, leider jedoch seit vielen Jahren vergriffen war. Es ist daher zu begrüßen, daß nun eine zweite Auflage erschienen ist, die inhaltlich stark erweitert und überarbeitet wurde, so daß nun eine aktualisierte Fassung dieses Standardwerkes vorliegt.
Die Aufteilung in 10 Kapitel wurde beibehalten: Spinnenmerkmale, funktio-