closely related species (*3*). Eighteen falling fights (grappling foundresses fell to the ground) between marked foundresses and potential joiners or usurpers were recorded at nests in sites 1 and 3; on two other occasions a single foundress was observed being killed by a usurper, which then replaced the dead wasp on the nest. Another single foundress remained on a nest as a subordinate after she was aggressively attacked by a wasp which then became the queen. Foundresses from three nests that had lost their broods to parasites were observed making repeated, unsuccessful attempts to either join or usurp remaining multiple-foundress colonies. In addition to the 18 falling fights of marked foundresses, nearly daily records of falling fights between unidentified gynes were noted at site 1, a habitat of high wasp density. Two foundresses were found dead in their nest boxes at site 1, and three injured foundresses were recorded at site 3.

Nest usurpation, in which a marked foundress was replaced by either a marked or unmarked foundress, was more common at single- than at multiple-foundress nests (Table 2, $P < .05$, paired-differences *t*-test and χ^2 contingency table). This conclusion is strengthened by the fact that the majority of usurpations of nests classified as multiple-foundress (36 of 60) occurred either before subordinates had joined the nest or after they had been lost. When usurpation occurred at a colony containing multiple foundresses, the usurper replaced a subordinate foundress. Nest usurpation was extremely frequent at site 1 and common at site 3, both habitats of high wasp density (Table 2). In fact, at site 1, only two triple-foundress nests displayed sufficient stability to allow ranking of foundresses in dominance. Minimal nest usurpation was recorded at site 5, the habitat of lowest wasp density. At site 5, wasps marked upon initiation of nests normally remained with their nests throughout the season.

Of 15 observations of conspecific nest intrusions into multiple-foundress colonies, the queen and her subordinates cooperated in defense five times. In the remaining ten observations, only one foundress was present on the nest during the intrusion. Here intruders were repelled by queens (six observations) or subordinates (four observations). In a series of experiments conducted before the emergence of the first workers, a live, tethered *P. metricus* gyne was presented to five different multiple-foundress colonies. In each presentation the tethered gyne was jointly attacked by the queen and her subordinates.

At low densities, single-foundress nests were nearly as productive as multiple-foundress colonies (Table 2). These findings are consistent with previous research at site 2 on *P. metricus* with similar wasp densities (*7*). In addition, a laboratory comparison of productivity in multiple- and single-foundress colonies of *P. fuscatus*, in which nest usurpation was prevented by experimental design, failed to detect significant productivity differences between multiple- and single-foundress colonies (*8*).

It is always to the queen's advantage, in terms of her longevity and the survival of the colony, to accept joiners. Queens of multiple-foundress colonies undoubtedly enjoy greater longevity than solitary foundresses because they spend more time on the nest and less time foraging (*9*). However, when wasp densities are low and nest usurpation infrequent, it is not advantageous for most foundresses, in terms of longevity and colony productivity, to join a more dominant foundress. Under these conditions, selection favors foundresses that initiate their own nests rather than join established colonies. If one makes the assumption that joiners are frequently sisters of the queen, it may be that the inclusive fitnesses of both queens and potential joiners are maximized by solitary nest founding at low frequencies of nest usurpation.

Under conditions of high wasp density and concomitant frequent nest usurpation it is in the best interest of less-dominant foundresses, in terms of longevity and colony productivity, to join an established queen rather than attempt to construct a nest. At high densities, single-foundress colonies have little chance of success, and foundresses frequently join established nests or attempt to usurp other colonies. It may be that other selective factors besides conspecific pressures provide an advantage to foundress cooperation in different habitats or for other species.

At high densities, single-foundress colonies, because of frequent nest inattendance or inability to defend against conspecifics, are especially vulnerable to usurpation. Several single-foundress colonies had a series of as many as eight different foundresses (queens) before the emergence of the first workers. When nests are usurped, foundresses use the future workers (brood) of presumably nonrelated gynes to rear their own reproductives. It is not surprising, in view of the aggressiveness of workers, that nest usurpation ceased at the appearance of the first workers.

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References and Notes

1. Defense against predation, increased competitive ability with conspecific individuals, increased feeding efficiency, penetration of new adaptive zones, increased reproductive efficiency, among others, have been suggested as prime movers of social evolution by E. O. Wilson [*The Insect Societies* (Belknap, Cambridge, Mass., 1971); *Sociobiology* (Belknap, Cambridge, Mass., 1975)].
2. R. D. Alexander, *Annu. Rev. Ecol. Syst.* **4**, 325 (1974).
3. The life cycle and behavior of *Polistes* wasps are discussed in detail by M. J. West Eberhard [*Misc. Publ. Mus. Zool. Univ. Mich.* **140**, 1 (1969)]. Subordinate *P. metricus* foundresses are normally driven from the nest by the queen about the time of first worker emergence (G. J. Gamboa, unpublished data).
4. Birds are common nest predators of *P. fuscatus* in Ontario, Canada (D. L. Gibo, personal communication).
5. P. Rau [*Ann. Entomol. Soc. Am.* **33**, 617 (1940)] reported that *P. pallipes* (=*P. metricus*) rarely built nests cooperatively, and M. K. Bohm [thesis, University of Kansas (1972)] recorded 8 of 91 *P. metricus* colonies as having multiple foundresses.
6. R. G. D. Steel and J. H. Torri, *Principles and Procedures of Statistics* (McGraw-Hill, New York, 1960).
7. In data gathered from five multiple- and five single-foundress colonies nesting in metal boxes (site 2) during the 1976 summer, the mean number of adults produced, 12.0 and 10.4, respectively, was not significantly different ($P < .5$).
8. D. L. Gibo, *Can. Entomol.* **106**, 101 (1974).
9. In approximately 65 hours of preemergence observations, triple-foundress, double-foundress, and single-foundress queens spent 5.33, 10.36, and 40.75 percent of their time off the nest.

10. I thank H. Dew for the use of the nest boxes she constructed at site 1; C. A. Callahan, J. Dropkin, B. Heacock, B. Sabel, and S. Wiltjer for their assistance in data collection; and C. D. Michener for his assistance and critical review of the manuscript. Partially supported by NSF grant BMS-75-07654; W. J. Bell and C. D. Michener, principal investigators.

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Handedness in Duckweed: Double Flowering Fronds Produce Right- and Left-Handed Lineages

Abstract. *Frond lineages of* Lemna perpusilla *Torr. (strain 6746) show handedness with respect to frond emergence sequence and flowering that is related to the pocket of origin on a double flowering mother frond. Flower position is a fundamental manifestation of frond asymmetry.*

The duckweed, *Lemna perpusilla* Torr. (strain 6746) (*1*) reproduces vegetatively through the production of daughter fronds at two meristematic areas (pockets) within the proximal end of a mother frond (Fig. 1a) (*2, 3*). Fronds of this clone are said to be left-handed because the first daughter frond emerges

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from the left pocket of a young mother frond and subsequent daughters emerge sequentially from right to left (*4–6*).

Frond asymmetry is also expressed in the flowering response in that flowers are ordinarily formed only in the right pocket of fronds exposed to inductive conditions when they are less than 80 μm in length (*7*). Because flowering is rarely observed in many species of *Lemna*, discussions of frond asymmetry have concentrated on frond emergence sequence; studies of asymmetry with respect to flower position have been neglected (*8*). Such an emphasis may be misleading since, under inductive conditions, flower development begins before the formation of any fronds within the same pocket (*2*, *3*). This suggests that the potential to flower on a given side is as fundamental an aspect of frond asymmetry as emergence sequence.

The production of a small percentage of fronds which bear flowers in both pockets is observed with prolonged subculturing under inductive conditions (Fig. 2) (*5*, *9*). To gain insight into mechanisms underlying frond asymmetry, I grew double flowering fronds (from which visible daughter fronds, if present, had been dissected) on medium solidified with agar (*10*). In this way I was able to follow frond emergence sequence and flowering in lineages arising from either pocket by observation under a dissecting microscope.

The lineages of fronds arising from the left pocket of a double flowering frond are right-handed, whereas those arising from the right pocket are left-handed (Fig. 1, b and c). In these figures handedness, that is, frond emergence sequence, is indicated by numbers (*11*). Such a relation is seen under both inductive and noninductive conditions and contrasts with the pattern observed with normal single flowering fronds where daughters produced at either pocket retain the handedness of the mother frond (*2–5*).

Since double flowering fronds initiate a dichotomy in the pattern of frond asymmetry in lineages arising therefrom and since flowers are formed before the formation of daughter fronds within any given pocket (*2*, *3*), it is clear that potential flower position and not frond emergence sequence is a fundamental determinant of frond asymmetry under both inductive and noninductive conditions (*12*). That is, in a normal single flowering lineage, a unique pattern of frond asymmetry is maintained because, during daughter frond ontogeny, flower position is determined in a way that is not dependent on the pocket of origin; fronds first emerge from the newly formed daughters at the nonfloral pockets, regardless of whether or not flower induction actually occurs. Double flowering upsets this pattern, giving rise to lineages that resemble their pocket of origin with respect to flower position. Frond emergence sequence is shifted accordingly.

Lemna perpusilla 6746 has proved useful for studies of photoperiodic floral induction and circadian rhythmicity (*13*). If determination of flower position is the principal component of frond emergence asymmetry (under both flowering and nonflowering conditions), this plant, with one potentially floral and one solely vegetative meristem, will also be useful for investigation of factors that commit plant meristems to different developmental pathways (*14*). Moreover, the presence of both floral and vegetative meristems on individual plants provides a convenient basis for study of the earliest events in floral evocation (*15*).

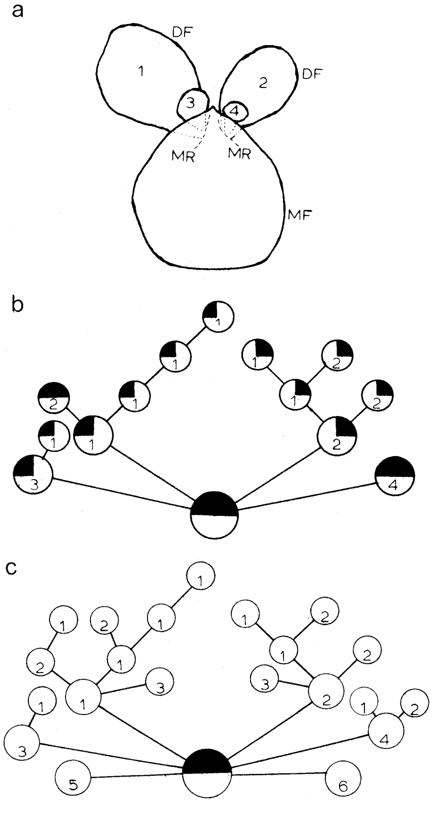

Fig. 1. (a) Diagrammatic view of the upper surface of a three-frond colony of *L. perpusilla* 6746 composed of mother frond (*MF*) and four daughter fronds (*DF*) arising from meristematic regions (*MR*). Numbers indicate frond emergence sequence (handedness). (b) Diagrammatic representation of frond lineages arising from double flowering fronds grown under inductive conditions. (c) Noninductive conditions. Frond emergence sequence (handedness) is indicated by numbers; shading indicates flower position (upper right, right pocket; upper left, left pocket; and upper half, both pockets).

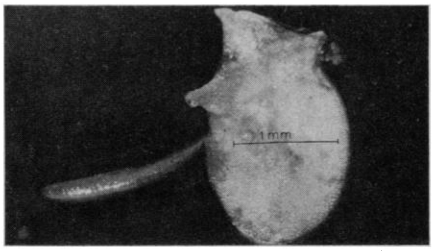

Fig. 2. Double flowering frond with daughter fronds removed. Pistils appear on both sides and stamens on right.

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References and Notes

1. R. Kandeler and B. Hügel [*Plant System. Evol.* **123**, 83 (1974)] state that this strain should be classified as *Lemna paucicostata* Hegelm., strain 6746. Accordingly, a few workers [for example, I. Yukawa and A. Takimoto, *Bot. Mag.* **89**, 241 (1976)] have adopted this species designation.
2. W. S. Hillman, *Bot. Rev.* **27**, 221 (1961).
3. ———, in *The Induction of Flowering*, L. T. Evans, Ed. (Cornell Univ. Press, Ithaca, N.Y., 1969), p. 186.
4. H. B. Posner, *Plant Cell Physiol.* **3**, 275 (1962); ——— and W. S. Hillman, *Am. J. Bot.* **47**, 506 (1960).
5. H. B. Posner, dissertation, Yale University (1962).
6. There is good evidence that frond emergence sequence, like many other handedness phenomena in plants, is not under genetic control. Thus, a 1 : 1 ratio of right- to left-handed fronds is observed in seedling strains obtained from self-pollination of *L. perpusilla* (*2*, *5*, *7*).
7. W. S. Hillman, *Am. J. Bot.* **46**, 466 (1959).
8. The rules used to designate the pattern of asymmetry reflect the emphasis on frond emergence sequence. See the first paragraph of this report.
9. Inductive photoperiodic cycles consisted of 8 hours of fluorescent light (1620 ± 540 lux) and 16 hours of darkness. Continuous light was used to grow noninduced plants. All cultures were grown in incubators at an air temperature of 26° ± 2°C.
10. I used half strength Hutner's solution containing 1 percent (weight to volume) sucrose and solidified with 1 percent (weight to volume) agar. This medium is described in (*3*).
11. Handedness of newly formed double flowering daughter fronds could not be determined since they produced no progeny during the course of the experiment.
12. F. H. Blodgett, *Bot. Gaz. Chicago* **60**, 383 (1915) states that fronds and flowers arise from the same meristematic area. He also notes that asymmetry is established at an early stage in frond ontogeny.
13. W. S. Hillman, *Science* **193**, 453 (1976).
14. Vernalization and phase-change both involve permanent conversion of the shoot meristem from the exclusively vegetative to the potentially floral condition. The features that distinguish apices that have undergone vernalization or phase change are very subtle, involving meristematic cells which, by definition, are undifferentiated [see C. F. Graham and P. F. Wareing, in *The Developmental Biology of Plants and Animals*, C. F. Graham and P. F. Wareing. Eds. (Saunders, Philadelphia, 1976), p. 44].
15. Evocation refers to the events that occur in the meristem leading to a switch from vegetative to floral morphogenesis [L. T. Evans, in *The Induction of Flowering*, L. T. Evans, Ed. (Cornell Univ. Press, Ithaca, N.Y., 1969), p. 457].
16. I thank Drs. R. M. Sachs and H. B. Posner for reviewing the manuscript. Some of the work reported here was carried out at the Department of Environmental Horticulture, University of California, Davis.

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