COMMUNAL ROOSTING IN RELATION TO WARNING COLOUR IN TWO HELICONIINE BUTTERFLIES (NYMPHALIDAE)[1]

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Communal roosting, reported for few butterfly species, appears to be of three types: (1) night-roosting, associated with repeated homing to the same roost, reported in acraeines, heliconiines, ithomiines and one nymphaline, and apparently occurring only in tropical species (Dewitz, 1877; Jones, 1930; Poulton, 1931; Carpenter, 1931; Moss, 1933; Beebe, 1950; Crane, 1957; Turner, 1971b; Benson & Emmel, 1973); (2) night-time aggregations of temperate grassland butterflies such as blues and satyrids (in Scotland I have noted several dozen *Coenonympha pamphilus* (L.) resting on the head of a flowering herb in late afternoon) which may result only from high population density; and (3) long-term aggregations during diapause, well known for the monarch (*Danaus plexippus* (L.)), and also observed in the tropical nymphaline *Smyrna karwinskii* (Geyer) (Muyshondt & Muyshondt, 1974), and the temperate arctiid moth *Euplagia quadripunctaria* Poda (Johnson et al., 1963). The function of these communes, whether night-roosts or diapause aggregations, is little understood, and it is not even clear how many species in what taxonomic groups have these habits, a situation complicated by the fact (K. S. Brown, pers. comm.) that some heliconiines which roost singly in some times and places, roost communally in others. I shall here discuss night-roosting only.

Two authors have proposed models of the ecology and evolution of tropical butterflies which link together, as part of the same complex of adaptations, communal night-roosting, restricted home range (with homing to roost), great adult longevity and high unpalatability (Benson, 1971; Turner, 1967, 1971a). Others have pointed out that the slow, steady, life-long rates of reproduction associated with these characters are adaptations to the slow but comparatively reliable production of resources needed by both adults and larvae which is characteristic of tropical forests (Benson & Emmel, 1973; Ehrlich & Gilbert, 1973).

Briefly, it is likely to be advantageous to organisms which have some

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protection such as an unpleasant flavour against predators to mass themselves gregariously in one place. In this way a predator which encounters one of them and experiments with tasting it will immediately encounter all the others and leave them alone, whereas if the prey were dispersed a number of them might fall victim to several different predators. This is particularly true if their predators are confined to home ranges, so that gregarious prey encounter fewer individual predators than dispersed prey do. Larvae can be gregarious from the mere laying of a clutch of eggs by the mother, but for butterflies to roost gregariously they must have some means of getting together every night; and it seems that the only way they can do this is by remembering the position of a roosting site. Hence, communal night-roosts will only be found in those species with a limited, learned home range in which they stay during the day, and individuals will tend to home to the same roost night after night. Butterflies that live only a few days are unlikely to learn home ranges or roosting positions, and the only way that night-roosts could develop in short lived or vagile species would be by the marking of the roost with a pheromone. Communication of this kind between unrelated individuals is probably very difficult to evolve. An experiment by Jones (1930) showed that *Heliconius charitonia* (L.) remember the position of their roosts, and do not use a pheromone. Communal roosters should therefore be sedentary and long lived, and great adult longevity coupled with restricted movement will produce the 'viscous' population structure likely to lead to the evolution of unpalatability through kin selection, thus bringing the adaptations full circle into an interlocking set. The evolution of this set of adaptations may be triggered by selection for slow sustained reproduction in the face of limited resources, and hence for great adult longevity, itself much enhanced if the adults are immune from attack by predators.

Thus it is predicted that communal night-roosts will be found in tropical butterflies which are unpalatable, long lived, have restricted home ranges and reproduce slowly. As knowledge of the roosting site is essential, it is further predicted that all communal roosters will repeatedly home to the same roost.

Communal roosting has long been known in heliconiine butterflies, which have the above characters to varying degrees, and it is the purpose of this note to record my observations of communal roosting in two of the less studied species. I have already mentioned these observations as "unpublished" in various papers, but feel that it may be helpful to set them down.

Observations

Heliconius ethilla (Godart) flies in the rainforests clothing the lower slopes of the Northern Range in Trinidad, where it has recently been the subject of a most elegant study on its longevity and home range behaviour by Ehrlich & Gilbert (1973). The only communal roost of this species which I have seen was in the lower canopy of the rainforest which formed a closed roof over parts of Andrew's Trace, where Ehrlich and Gilbert carried out their experiments. At 1745 ST on 12 August 1964, I observed a number of this species fluttering around a group of leafless twigs in the canopy in the way that is characteristic of *Heliconius* when they are preparing to roost for the night. Occasionally some of them would flutter lower onto the vegetation at the edge of the path. By 1815 ST all had settled on the twigs and the dusk in the forest had become quite deep. I returned at midnight that night and was able with glasses to count seven roosting butterflies. I became somewhat concerned about their identity, because around 1800 ST I had been able to net one of the butterflies flying beneath the roost at the edge of the path, and this turned out to be *Tithorea harmonia* (Cramer), the muellerian comimic of *H. ethilla.*

Doubts about the identity of the butterflies in the roost were dispelled on 15 August when at 2300 ST in heavy rain I was able to observe the roost with a small but powerful telescope; it contained seven undoubted *Heliconius ethilla* and no *Tithorea.* The *Tithorea,* which had been captured during the previous observations, had been kept in one of the New York Zoological Society's insectaries at Simla in the interim and had been marked and released, along with another individual from just north of Port of Spain, immediately below the site of the *H. ethilla* roost at around mid-day on 15 August. Neither of these butterflies was in the roost when it was observed at 2300 ST, and I concluded that this particular roost consisted entirely of the *Heliconius.* It would be interesting to know if the comimics ever do roost together. (*T. harmonia* has been observed in roosts of *Heliconius erato* in Brasil as reported by Vasconcelos Neto & Brown, pers. comm.). I last observed the roost on 27 August, when it was still occupied.

Dryadula phaetusa is one of the heliconiines which have departed rather little from the nymphalid appearance which one assumes is the ancestral form of the whole group. Yet it too appears to have developed the habit of communal roosting which is little known in the rest of the nymphalids. I did not succeed in making any observations of this species roosting in the wild, but while preparing to carry out some observations on its courtship for Miss Jocelyn Crane at the New York

Zoological Society's Research Station, I kept half a dozen males in one of the extremely large cages (20′ × 30′ × 20′) which were used for observations of this kind. One evening at dusk Miss Crane noted that the butterflies appeared to be roosting communally in the cage. I was able to observe and photograph this on subsequent evenings. The floor of the cage was grassy, and the males were indulging in typical heliconiine roosting behaviour, fluttering around blades of grass and eventually settling, most of them lined up with their heads pointing in the same direction on the underside of the same large grass blade. It seems likely that this is their normal method of roosting, as *D. phaetusa* is a butterfly of comparatively open country, unlike many of the heliconiines which prefer densely wooded growth and roost either on dried twigs as described above or on the remains of dried creepers hanging from trees. My observation of communally roosting *Heliconius* in cages where they do not have the twigs or the vines, is that they roost more or less aggregated on the fabric or wire either of the roof or the sides of the cage at some distance from the ground, and never attempt to roost on the ground vegetation as the *D. phaetusa* were doing. The *D. phaetusa* on the other hand were never observed roosting on the roof or the sides of the cage, which leads me to believe that roosting on grass blades or other green vegetation is normal for them in the wild. (I understand from correspondence that this has been confirmed in the wild by Benson.)

DISCUSSION

Heliconius ethilla fits well into the above theories about the functional value of communal roosting. It is not known whether it homes to the roost, but it does have a strictly patrolled home range and is one of the most unpalatable members of the genus (Ehrlich & Gilbert, 1973; Brower, Brower & Collins, 1963). Its confirmed longevity and slow rate of reproduction were used by Ehrlich & Gilbert as the basis for their model of adaptation in tropical forest butterflies. Both *Heliconius erato* (L.) (unpalatable, home range, long lived) and *H. charitonia* (palatability and home range unknown, probably long lived) show a strong tendency to home to the same roost (Jones, 1930; Beebe, 1950; Turner, 1971b). *Heliconius melpomene* (L.) and *H. sara* (Fabricius) both roost communally and are both unpalatable.

Very little is known about *Dryadula phaetusa*; its palatability, longevity, home range and roost-homing have not been investigated. Among the known palatable heliconiines, *Agraulis vanillae* (L.) and *Dryas iulia* (Fabricius), there is little or no tendency to roost communally (Crane, 1957). There is one casual observation which suggests that *D. phaetusa* is long lived. *Heliconius* species require, for reasons that are controversial, a source of amino acids, which they obtain from pollen; this need seems to arise from the long adult life-span (Gilbert, 1972). On Barro Colorado Island (Canal Zone) in 1975, I observed a male *D. phaetusa* palpating a bird-dropping with his proboscis; Brown (1973) has photographed the same behaviour in *Heliconius aliphera* (Godart) in Brasil (I have noted this also in Panamá), and it presumably shows that the butterfly requires amino acids or other nitrogen compounds.

D. phaetusa, more than any other heliconiine, has the rounded wings and rather dull colour (particularly in the female) typical of nymphalines; it has all the appearance of a "primitive" species. However, in its roosting behaviour it is clearly not "primitive", and this term should only be used of particular characters, never as a blanket term for a whole species. It does have two striking similarities to *Marpesia berania* (Hewitson), the only nymphaline known to roost communally, which in accord with the model, is very long lived and homes faithfully to its roost (Benson & Emmel, 1972). Both species are orange-brown, rather than obviously warningly coloured, and both are sexually dimorphic, with duller-coloured females. This strongly suggests that communal roosting and at least some of the habits that go with it are not necessarily accompanied by unpalatability.

CONCLUSIONS AND SUMMARY

Communal roosting for the night seems to occur only in tropical butterflies which are of low vagility and which are long lived; in all cases investigated it has been found that the individual butterflies tend to home repeatedly to the same roost. This is expected in theory and what is known of the biology of *Heliconius ethilla* and *Dryadula phaetusa*, whose communal roosting as reported here, tallies with this generalisation. The suggestion that communal roosting is associated with unpalatability may or may not be true in general: the heliconiine *D. phaetusa* and the nymphaline *Marpesia beriana*, both communal roosters, are not obviously warningly coloured and may be palatable.

The communal roosting of both temperate and tropical butterflies and moths during diapause is obviously a rather different phenomenon.

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