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THE EVOLUTION OF GREGARIOUSNESS IN DISTASTEFUL INSECTS AS A DEFENSE AGAINST PREDATORS

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Many animals live in groups, and gregariousness may evolve as a means of defense against predation. Although a group should be easily discovered, group members may suffer a lower risk of being attacked because of several factors including increased vigilance and defense (Bertram 1978). Another benefit that may accrue from gregariousness is that the risk of being attacked for any particular prey individual is decreased when surrounded by others. This effect, termed "dilution" (Bertram 1978), is purely statistical and does not require any complex or cooperative behavior. Treisman (1975) and, more recently, G. Turner and Pitcher (1986) have modeled the evolution of gregariousness in terms of detection risk and dilution.

The value of dilution depends on the properties of group-living prey that are highly variable. In fish and mammals, for instance, a predator encounter may result in one or very few specimens being taken, either through the escape of non-attacked prey or through predator satiation (Bertram 1978; G. Turner and Pitcher 1986). In these cases, prey agility or large size results in a lowered predation risk for the group mates of an attacked individual. Other prey types living in exposed groups, like many insects, are both small and slow in relation to many potential predators. With such prey, a predator should have the capacity to consume an entire group once discovered. How can gregariousness evolve in such organisms?

Among insects, unpalatability and aposematic coloration are common defenses against predators. The effectiveness of such defenses depends on the spatial distribution of prey organisms. A predator learns through experience not to attack members of a distasteful species, and it is then advantageous for the prey to congregate in as few predator feeding territories as possible (Treisman 1975; J. Turner 1975; Leimar et al. 1986).

The spatial distribution of prey within a predator feeding area may further affect its survival. In this paper we apply the ideas of G. Turner and Pitcher (1986) and show how various properties such as unpalatability and aposematic coloration of prey influence the evolution of gregariousness. The theoretical analysis gives rise to a number of predictions; for instance, our model shows that predation may result in disruptive selection on prey group size, yielding the expectation that

distasteful prey species should either be solitary or live in fairly large groups. Finally, we discuss how well our model's predictions are met in nature.

A MODEL OF PREDATOR DISCOVERY AND ATTACK

The effect of grouping of small and relatively slow prey organisms on the rate of death from predation can be analyzed as the combination of two factors. A group is likely to be more conspicuous than a single individual and is then more easily discovered by a predator. Since the discovery of the group and all group members are simultaneous events, this first factor represents a disadvantage for a group member by increasing its rate of detection above that of a solitary individual. However, given discovery, the probability of being attacked may be lower for a group member than for a solitary individual; this benefit must outweigh the disadvantage of conspicuousness for group living to be advantageous.

That the balance of these two factors is crucial is implicit in some previous work on the evolution of gregariousness (Treisman 1975; Bertram 1978). G. Turner and Pitcher (1986) gave a more direct analysis of the effect and coined the term "attack abatement" for the influence of group living on the combination of discovery and attack once discovered. The following model of predator discovery and attack investigates the influence of distastefulness and warning coloration on the evolution of gregariousness.

We first consider the rate of detection. Empirical information on how visual detection depends on the size of an object is available mainly from studies on humans (Vine 1973; Treisman 1975). An observer's chance of detecting an object increases roughly in proportion to the solid angle it subtends as seen by the observer as long as the angle is small, but the increase levels off for larger solid angles. We use

$$R(n) = A(1 - e^{-n/n'}) \quad (1)$$

for a predator's rate of detection of a group containing n prey (i.e., for a short time interval, t , the probability of detection is Rt). For n much smaller than n' , the rate of detection is approximately proportional to group size ($R = An/n'$); and as n gets much larger than n' , it approaches the asymptote $R = A$. The parameter n' can be regarded as a "threshold group size," at which R begins to level off. Expression (1) for the rate of detection is qualitatively similar to the probability of detection assumed by Treisman (1975) and based on experiments on visual detection in humans when the area that a group exposes to a predator is proportional to group size.

The disadvantage of an increased rate of detection that results from group living is smaller when R levels off more quickly. For equation (1) this corresponds to smaller n' . Also, if the area that a group exposes to a predator is less than proportional to group size (not covered by eq. 1), the disadvantage is smaller. Moreover, the coloration of prey affects the rate of detection. According to Treisman (1975) the main effect of a conspicuous prey coloration is to increase the parameter A in equation (1). Since change in A yields the same relative change in

rate of detection of solitary individuals and groups, it does not affect the value of group living. Whether prey coloration also affects the parameter n' in our model is less clear.

To obtain an expression for the probability of attack given discovery, we use a simple model of predator avoidance learning. It is known empirically that, when a naive predator encounters a group of distasteful prey items, it typically attacks a few individuals before learning to avoid them (Gittleman and Harvey 1980). One way of modeling this process is to assume that for each attack there is a probability h that the predator becomes inhibited from further attacks (see the model in Leimar et al. 1986). The probability that the predator samples m prey individuals before learning to avoid them then becomes

$$(1 - h)^{m-1}h, \quad (2)$$

assuming that a sufficient supply of prey individuals is available. With this distribution, the expected number of prey sampled before avoidance equals $1/h$. For a small group, all the prey may be sampled without producing avoidance. By using the distribution (2), it is straightforward to compute the expected proportion attacked when a group of n individuals is discovered by a naive predator as

$$P(n) = [1 - (1 - h)^n]/nh. \quad (3)$$

Note that $P(1) = 1$ and that $P(n)$ approaches $1/nh$ as n becomes large.

The inhibitory effect of an attack (h) depends both on the distastefulness and on the coloration of prey. Typically, h increases both with increasing distastefulness and with more-conspicuous coloration (Leimar et al. 1986).

We now compute the rate of death for individuals in groups of differing sizes. Putting equations (1) and (3) together yields the expression

$$D(n) = R(n)P(n) = A(1 - e^{-n/n'})[1 - (1 - h)^n]/nh, \quad (4)$$

for the rate of death of an individual living in a group of size n in the feeding territory of a naive predator (i.e., for a short time interval t the probability of death is Dt). As time passes, the probability that the predator has become inhibited increases, causing D to decrease. For simplicity, we use the initial death rate (eq. 4) to evaluate the effects of group size.

In figure 1 we show D as a function of n for a particular choice of the parameters h and n' . Note that D first increases from $D(1)$ but then decreases and eventually falls below $D(1)$. We would expect that this kind of shape of $D(n)$ is a general consequence of the effects of group size on the rate of detection and on attack dilution and is not limited to the particular model we consider. It has not been noted previously that solitary individuals may survive better than members of small groups but worse than members of larger groups; one has generally assumed that advantages of group living are already present for small groups (see, e.g., Bertram 1978).

We then conclude that above a certain minimum group size the rate of death from predation of group members falls below that of solitary individuals. If n increases beyond this value, D decreases further and there is no optimum group

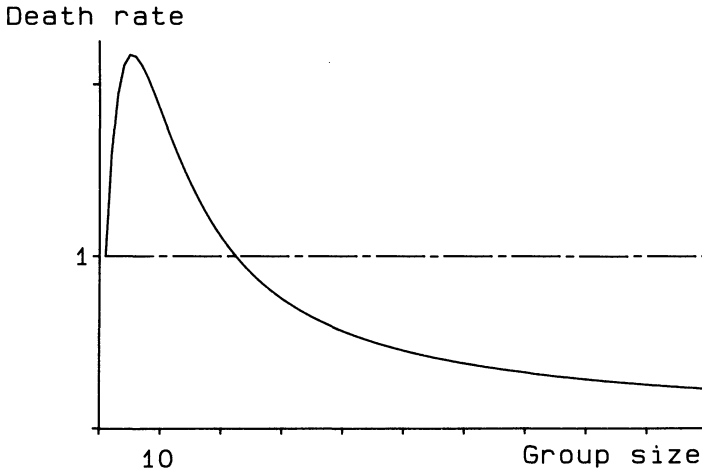


FIG. 1.—The curve shows the rate of death from predation, $D(n)$ in equation (4), as a function of the size (n) of an aggregation. The parameters in equation (4) are $h = 0.2$, $n' = 4$, and A to make $D(1) = 1$. $D(n)$ decreases below $D(1)$ at $n = 23$.

TABLE 1
MINIMUM GROUP SIZE NECESSARY FOR GROUP LIVING TO BE ADVANTAGEOUS

NO. OF ATTACKED PREY (1/h)	"THRESHOLD GROUP SIZE" FOR DETECTION RATE (n')*								
	1	2	4	8	16	32	64	128	256
1	2	2	2	2	2	2	2	2	2
5	6	12	23	43	83	162	321	639	1274
10	11	24	45	86	166	326	645	1285	2565
50	51	115	224	426	826	1626	3226	6426	12826
100	101	229	448	851	1651	3251	6451	12851	25651

* n' indicates the group size for which the detection rate starts leveling off toward an asymptote.

size. However, the minimum group size is important since factors such as food availability or, for groups of larvae, female fecundity might set an upper limit to group size. This upper limit ought then to exceed the minimum for gregariousness to be advantageous.

Minimum group size depends on the characteristics of the function $D(n)$. In table 1, we illustrate how minimum group size depends on the parameters h and n' . As might be expected, minimum group size is small when there is both a strong inhibitory effect (h close to one) and a small penalty in the rate of detection when n increases (n' small).

When writing $D(n)$ as a product of rate of detection and probability of attack, we have assumed that prey are always killed when attacked. However, it is known (Wiklund and Järvi 1982) that distasteful prey often survive attacks by predators, and equation (4) could be modified by multiplying the right-hand side with a probability of death in an attack. If this probability is the same for grouped and

solitary individuals, such a modification does not change the minimum group size. The important effect of distastefulness on group size is that it causes attacks by the predator to inhibit further attacks, not that it may increase survival in an attack.

Similarly, the conspicuousness of a single individual affects the minimum group size only to the extent that it has an influence on the increase of R with n or on the inhibitory effect of an attack.

We have used the initial death rate, D , to evaluate the effects of grouping. A more extensive model should take into account the presence of the predator in its feeding territory over a period of time. If several groups with possibly varying sizes exist in the territory, an interaction among groups is introduced. Individuals in one group may be attacked and thus inhibit the predator from attacking individuals in other groups. We have developed such a model along the lines of an earlier model of predator-prey interaction (Leimar et al. 1986). The resulting minimum group size that was stable against invasion by "solitary strategists" turned out to be slightly larger than that obtained from equation (4), because a solitary individual shares the territory with more or bigger groups and thus is more "protected" than a group member. Since the model is fairly complicated and the effect on minimum group size is small, we do not present the details.

Sibly (1983) emphasized the difference between optimum group size and evolutionarily stable group size and suggested that stable group size should exceed the optimum. The situation we have analyzed differs from the one considered by Sibly, first because in our model group living may not be advantageous for small groups (fig. 1) and second because we have not introduced any factors (unrelated to predation) that reduce fitness of members of very large groups. If an individual is given the strategic options of either joining an already existing group or living solitarily, the curve $D(n)$ in figure 1 corresponds to two evolutionarily stable strategies (ESS's): living alone and living in a single group. However, there is no solitary ESS if a group above minimum size can be formed in a single step (e.g., through egg clustering). The strategy of living in one group may shift to a strategy of living in several smaller groups when non-predatory factors limiting group size are taken into account. This strategy may disappear if such effects are strong enough, leaving solitary living as the only ESS.

In this connection it may be of interest to make a comparison with Hamilton's (1971) "selfish herd" model. Being solitary is not an ESS in that model, since a prey individual tends to reduce a "domain of danger" by moving close to, say, the nearest neighbor. Our assumptions about predator behavior differ substantially from those made by Hamilton; the main differences are that we assume that the predator must detect prey before attacking and that the probability of detection depends on group size. Thus, a prey individual that attaches itself to a conspecific will (approximately) double its rate of detection, and if there is a chance that a predator attacks both individuals in such a pair ($h < 1$), the prey will be at a disadvantage. Hamilton (1971) also suggested that gregariousness is stabilized by predation on marginal individuals and may well result in a lower mean fitness of prey individuals. In our model, group living is stable only when it reduces the

overall rate of death from predation; this is also true when the risk of predation is greater for marginal than for central group members.

DISCUSSION

The model in this paper deals with prey organisms that live exposed, have no means of escape when discovered by a predator, and are small in relation to a potential predator, which in effect means that a predator can sample many prey individuals in one encounter. For such prey, distastefulness is an important condition for the evolution of gregariousness in that it acts like a predator-satiation mechanism, thereby making a dilution effect possible. The more prey specimens that the predator needs to sample during avoidance learning, which in turn depends on both the distastefulness (Alcock 1970; Goodale and Sneddon 1977) and the coloration (Gittleman and Harvey 1980; Sillén-Tullberg 1985) of prey individuals, the larger an aggregation needs to be in order for gregariousness to be advantageous (table 1). Thus, palatable prey need to live in "infinitely" large groups, or rather, the aggregations must be so large that predator satiation is independent of distastefulness (as might be the case for periodical cicadas; Lloyd and Dybas 1966). Another important condition for the evolution of gregariousness is, in accordance with G. Turner and Pitcher (1986), that predator discovery does not increase too much with group size (table 1). If it is possible to live in a group without any increase in discovery, as may be the case for some nonexposed prey, there is no cost of gregariousness even for entirely edible prey.

For an already gregarious species, selection resulting from predation favors further increases in group size (fig. 1). For instance, Calvert et al. (1979) showed that the frequency of predation among monarch butterfly aggregations was inversely related to aggregation size. However, factors other than predation may limit natural group sizes. For example, larval group size in insects, which often is a consequence of egg-cluster size (Stamp 1980), may be related to female fecundity and/or larval resource utilization (Hebert 1983; Young 1983; Parker and Courtney 1984).

Our analysis gives rise to a number of predictions concerning aggregations in natural populations, of which the following are the most important.

1. Gregarious species that live exposed in moderately large groups and are relatively small and slow ought to be distasteful to potential predators; they should also have been distasteful at the time when they evolved gregariousness.

2. Because of disruptive selection on group size (fig. 1), one would expect the distribution of group sizes among species to show a bimodal pattern, one mode at solitary individuals and one at fairly large groups.

3. Because of selection for increasing group size in gregarious organisms, organisms that have fewer constraints (unrelated to predation) on the maximum group size are expected to show the largest aggregations.

We now discuss how well these predictions bear out. First, are gregarious species often distasteful? It has been known for some time that gregarious species generally are aposematic (Poulton 1890; Fisher 1930; Cott 1940; Rettenmeyer

1970; Edmunds 1974), and the distasteful quality of some of these organisms has been verified in experiments with predators (Brower 1958; Sillén-Tullberg et al. 1982) or inferred from the use of poisonous host plants, the emission of noxious substances, or the possession of defensive structures (Cott 1940; Ehrlich and Raven 1965; Wood 1977).

Two main reasons for aggregation in these organisms are commonly given: gregariousness increases the aposematic signal (Poulton 1890; Beddard 1895; Cott 1940; Wilson 1975), and it increases chemical or structural defense possibilities (Cott 1940; Wilson 1975; Aldrich and Blum 1978; Howard et al. 1983). Both of these benefits of group living are plausible, although both need to be tested experimentally (Sillén-Tullberg, MS). The theoretical model presented here shows that neither of these "extra" advantages is necessary for the evolution of gregariousness since distastefulness per se may be enough. However, as we have mentioned, it might be easier for gregariousness to evolve in already aposematic organisms because conspicuous coloration decreases the number of individuals sampled by a predator during avoidance learning (Sillén-Tullberg 1985).

According to our first prediction, the evolution of distastefulness should precede gregariousness (see also Sillén-Tullberg and Bryant 1983; J. Turner 1984*a,b*). This seems to have been the case in butterfly larvae. In a recent study based on phylogenetic analysis (Sillén-Tullberg 1988), distastefulness invariably preceded gregariousness for lineages in which both distastefulness (inferred from aposematic coloration) and gregariousness had evolved and where the two evolutionary events could be separated.

Our second prediction concerns the distribution of group sizes among species. One way to investigate this is to look at the egg-laying pattern (and concomitant larval group size) of related species using the same host plant: three Scandinavian *Pieris* species live on *Brassica* and other cruciferous plants; *P. rapae* and *P. napi* both lay solitary eggs; and *P. brassicae* lays batches of 30–80 eggs (Henriksen and Kreutzer 1982). Similarly, for Scandinavian Nymphalinae using stinging nettle (*Urtica dioica*), two species lay solitary eggs (*Polygonia c-album* and *Vanessa atalanta*), and three species lay batches of 30–80 (*Aglais urticae*), up to 300 (*Inachis io*), and over 100 eggs (*Araschnia levana*), respectively (Henriksen and Kreutzer 1982). This clearly demonstrates the dichotomy between laying solitary eggs on the one hand and fairly large batches on the other.

We have also chosen two larger samples of species to illustrate the bimodal form of the distribution of group sizes. The first sample, from Hebert (1983), consists of moth larvae (fig. 2); for the second sample, of larvae of North American Nymphalinae (fig. 3), the data on cluster sizes have been derived from Scott (1986; see the Appendix). Both distributions show a high frequency of species with solitary larvae, a high frequency of species with large groups, and relatively few species with intermediate group sizes. The upper limit for group sizes in both of these samples is probably set by factors that are unrelated to predation, for example, female fecundity or larval resources.

In the life cycles of insects, there are two main categories of aggregations. Adult aggregations are usually formed in connection with inactive phases in life, such as

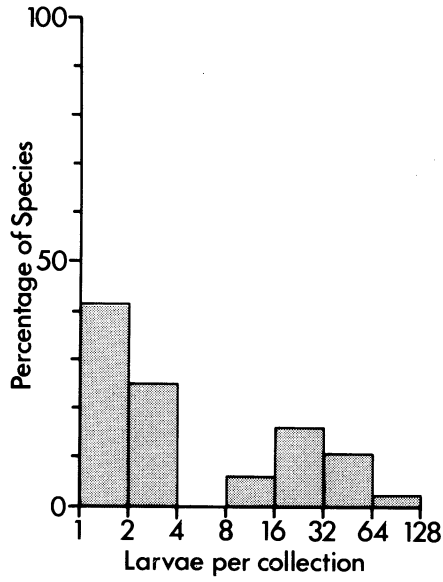


FIG. 2.—The distribution of larval abundances for 61 species of Canadian Lepidoptera with reduced mouthparts. Families that lack functional mouthparts have a high representation of gregarious species. (After Hebert 1983.)

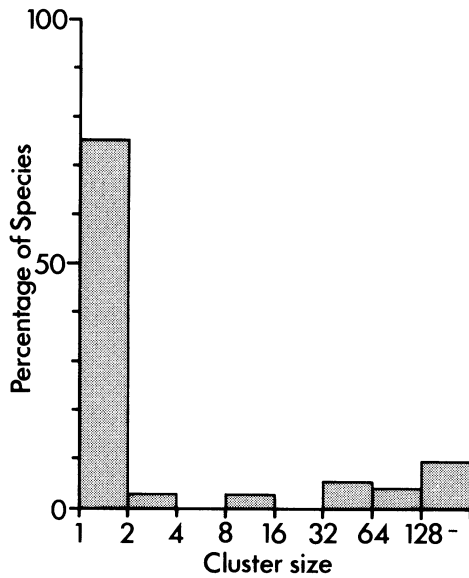


FIG. 3.—The distribution of egg-cluster size as a measure of larval gregariousness in North American Nymphalinae. Data from Scott (1986); see the Appendix.

roosting and hibernation (J. Turner 1975; Monteith 1982; Malcolm 1987), and come about through active migration of the participating individuals. Larval aggregations, on the other hand, come about through the female's clustering of her eggs (Stamp 1980), and since this type of aggregation consists of feeding and growing organisms, its size is much more likely to be food-limited. It is therefore interesting to note the great difference in size attained by larval aggregations on one hand and adult, especially hibernating, aggregations on the other. Although larval aggregations seldom exceed a couple of hundred individuals (see figs. 2, 3), aggregations of hibernating adults may amount to thousands, tens of thousands, and sometimes millions of individuals (Johnson et al. 1963; Hodek 1973; Brown and Vasconcellos Neto 1976; Solbreck 1976; Urquhart 1976; Lee 1980; Monteith 1982; Wolda and Denlinger 1984). We suggest that this difference between larval and adult aggregations, in line with our third prediction, arises because larval group size is more severely limited by factors unrelated to predation. Adult roosting assemblages (Alcock 1972; J. Turner 1975; Mallet 1986) generally are smaller than hibernation aggregations, which could be an effect of their temporary nature and the fact that they basically consist of reproductive, resource-limited individuals.

Although larval aggregations as a rule are smaller than adult ones, our impression from the literature is that the phenomenon of gregariousness is more common in insect larvae than in adults. It is therefore worth noting that the difference in the way adult and larval aggregations are formed may have a bearing on their frequency of occurrence. By clustering her eggs, a female could easily bring about a larval aggregation of the required minimum size. Adult congregation, however, requires each participating individual to locate other individuals or specific aggregation sites. Bringing about adult aggregations may therefore be more difficult since they require behavioral synchronization among individuals.

In line with G. Turner and Pitcher (1986), this paper offers a general explanation for the evolution of gregariousness in insects, without invoking complex behaviors such as synchronized defense. As pointed out by Chew and Robbins (1984), many advantages of group living that are observed in gregarious insects—for instance, increased feeding efficiency—are likely to be secondarily evolved traits rather than the original reasons for gregariousness. Similarly, communal defense behaviors such as synchronized signaling or emitting noxious substances (Prop 1960; Aldrich and Blum 1978) have most likely evolved secondarily to gregariousness.

SUMMARY

Many insect species form aggregations in either the larval or adult stage. The evolution of gregariousness in insects may seem disadvantageous because aggregations are easily discovered by a predator and because insects are small and slow in relation to many potential predators that then have the capacity to consume an entire group. For animals in general, a benefit of group living may be a decreased risk of predator attack on any particular individual. For insects, this effect, called

dilution, can be a consequence of distastefulness, which limits the number of prey that a predator can take.

A model is developed in which we vary the risk of detection in relation to group size and the degree of prey distastefulness and aposematic coloration, both of which affect the number of prey a predator samples during avoidance learning. According to the model, members of small groups may have a higher rate of death from predation than solitary individuals, but above a certain minimum group size, group members do better than solitary individuals. As group size increases above the minimum value, group members suffer fewer and fewer deaths from predation. However, other factors, unrelated to predation, constrain group size. For gregariousness to be advantageous, such constraints must be weak enough to allow groups larger than the minimum size.

Our model predicts that (1) gregarious insect species should be distasteful, and the evolution of distastefulness should precede that of gregariousness; (2) the distribution of group sizes among species should show a bimodal form; and (3) the largest aggregations should be found in forms that have fewer constraints unrelated to predation on group size. The agreement between these predictions and data is discussed.

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APPENDIX

Data on egg-cluster size in North American Nymphalinae are derived from Scott (1986), who provided data on the number of eggs per batch for 73 species. Most species lay single eggs, but some of these (marked with asterisk below) are reported to lay a few eggs together occasionally. For species that are batch layers, we have used the average batch size whenever mentioned, but for most species we have taken the mid-range value of batch sizes.

Single eggs: *Limenitis archippus*, *L. arthemis*, *L. weidemeyerii*, *L. lorquini*, *L. bredowii*, *Epiphile adrasta*, *Dynamine dyonis*, *Hamadryas februa**, *Ha. guatemalena**, *Ha. iphithime*, *Smyrna karwinskii*, *Historis odius*, *Siproeta stelenes**, *Anartia fatima*, *A. lytrea*, *A. jatrophae*, *Precis coenia*, *Pr. evarete*, *Pr. genoveva*, *Vanessa atalanta*, *V. tameamea*, *V. cardui*, *V. virginiensis*, *V. carye*, *Polygonia interrogationis**, *Po. comma**, *Po. satyrus**, *Po. progne*, *Po. faunis*, *Boloria selene*, *B. titania*, *B. improba*, *B. freija*, *Speyeria diana*, *Sp. aphrodite*, *Sp. cybele*, *Sp. nokomis*, *Sp. idalia*, *Sp. mormonia*, *Sp. adiate*, *Sp. hydaspes*, *Sp. callippe*, *Sp. atlantis*, *Sp. egleis*, *Sp. zerene*, *Sp. coronis*, *Sp. edwardsii*, *Euptoieta claudia*, *Dryadula phaetusa*, *Dione vanillae*, *Di. moneta**, *Dryas iulia*, *Heliconius isabella**, *He. charitonia**, *He. erato*.

2–3 eggs per batch: *Biblis hyperia*, *Boloria eunomia*.

8–15 eggs per batch: *Hamadryas fornax*, *Boloria polaris*.

32–63 eggs per batch: *Poladryas minuta*, *Phyciodes morpheus*, *Ph. tharos*, *Ph. frisia*.

64–127 eggs per batch: *Hamadryas amphinome*, *Chlosyne nycteis*, *Phyciodes picta*.

≥128 eggs per batch: *Nymphalis milberti*, *N. antiopa*, *Euphydryas phaeton*, *E. editha*, *E. gillettii*, *Chlosyne lacinia*, *C. harrisii*.

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