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TERRITORIAL BEHAVIOR OF *NYMPHALIS ANTIOPA* AND *POLYGONIA COMMA* (NYMPHALIDAE)

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ABSTRACT. The behavior of perching *Nymphalis antiopa* and *Polygonia comma* is described. Males of both species occupy and defend specific areas or territories. Territories of *N. antiopa* are much larger than those of *P. comma*. *P. comma* males, like *Vanessa atalanta,* patrol and defend the same areas. In contrast, *N. antiopa* males defend areas much larger than areas patrolled and change perch sites frequently. Territorial behavior of these two species and that of *V. atalanta* are compared and attempts are made to explain differences among the three species on the basis of varying degrees of competition for mating sites and females.

Male butterflies adopt one of two general strategies for locating mates, perching or patrolling (Scott, 1974). Patrolling species search for females, whereas perching species perch on trees, bushes, herbs or the ground and wait for females to fly by. Many of the fast flying, relatively short-winged nymphalids are perching species (Joy, 1902; Shields, 1967; Baker, 1972; Dimock, 1978; Bitzer & Shaw, 1979(80)). Nymphalids and other perching butterflies vary in the degree of site attachment and in the intensity with which they pursue butterflies that pass near their perches. This has led to a controversy over whether male butterflies show true territorial behavior (Baker, op. cit.; Scott, op. cit.; Silbergleid, 1977; Davies, 1978; Bitzer & Shaw, op. cit.).

We have described territorial behavior in the nymphalid, *Vanessa atalanta* (L.) (Bitzer & Shaw, op. cit.). Territorial behavior in this species is characterized by 1) outlining territories by intermittent patrols, 2) perching on one or two specific sites within territories and 3) chasing all intruders, including conspecifics, butterflies of other species and birds. Conspecifics are chased vertically in a characteristic spiral, while other species of butterflies and birds are chased horizontally to the limits of the territorial boundary. In this study we describe territorial behavior of two other nymphalids, *Nymphalis antiopa* (L.) and *Polygonia comma* Harris.

TABLE 1. Characteristics of nymphalid territorial behavior.

Species	Territory size (m)	Area (m) patrolled	% males patrolled	Patrolling frequency (%)	Patrol duration (s)	Interaction frequency (/h)	No. perch sites/territory
N. antiopa	308 ± 124.7 (28–43 × 6–13) N = 5[b]	[a] (1–11 × 1–3) N = 5	100 N = 5	16.2 (13.2 & 21.3) N = 2 n = 66[c]	12.1 ± 9.6 (2–58) N = 2 n = 66	1.8 ± 2.0 (0.3–4.7) N = 4 n = 12	many
P. comma	12.0 ± 5.9 (3–10 × 2–4) N = 10	12.0 ± 5.9 (3–10 × 2–4) N = 10	47 N = 10	6.2 ± 3.7 (3.1–12) N = 5	18.8 ± 25.4 (4–180) N = 5 n = 28	4.9 ± 4.4 (0–10.4) N = 8 n = 43	1–3
V. atalanta	86.6 ± 45.3 (7–37 × 4–11) N = 29	86.6 ± 45.3 (7–37 × 4–11) N = 29	100 N = 26	9.4 ± 4.6 (1–17) N = 26 n = 420	17.2 ± 18.7 (5–70) N = 26 n = 369	23.6 ± 21.5 (0–82) N = 24 n = 1218	1–2

[a] Data insufficient to determine area patrolled.
[b] N = number of animals.
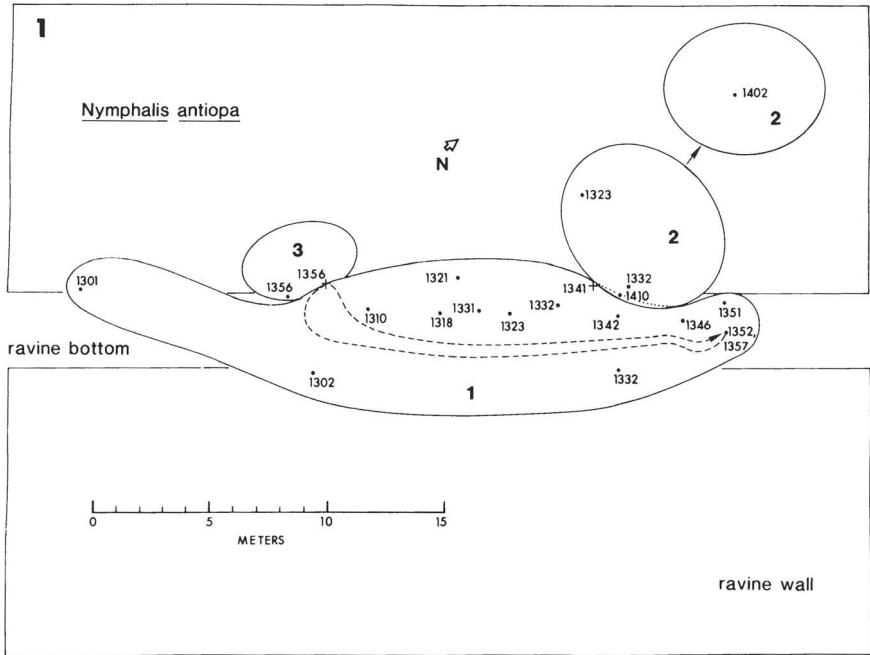[c] n = number of events.

FIG. 1. Perching sites of *N. antiopa* males in ravine on 21 April 1979. Diagram shows southwest three-quarters of ravine: (●) perch sites at indicated times (CST); (——) total areas defended and patrolled by males identified by number; (+) site of interaction between adjacent males at indicated times; (–––) flight path of male #1 to site of interaction with male #3 and back to same resting spot; (·····) boundary of territory #1 within boundary of territory #2.

OBSERVATIONS

Nymphalis antiopa

N. antiopa males were observed in a ravine (46 m long, 28 m wide) in Railroad Park, Ames, Iowa (a wooded, hilly area, 51.8 hectares) on 8 April 1977 and 14, 18 and 21 April 1979. Males entered the ravine between 1130 h and 1200 h (CST) and departed between 1530 h and 1600 h. Males chased other *N. antiopa* and other species of butterflies and birds from territories averaging 308 ± 124.7 m² (Table 1). Occupants flew short patrols every few minutes, outlining areas much smaller than the area defended (Table 1). After a patrol, males seldom returned to the same perch (Fig. 1). On 21 April, during 30 successive landings, a territorial male landed 0–11 m ($\bar{x}$ ± S.D. = 3.06 ± 2.36 m) from his previous perch, returning to the same perch only twice.

On 18 and 21 April, males averaged 16.2 patrols/h (64 in 244 min) (Table 1) and 1.4% of their site occupation time (3.3 of 244 min) pa-
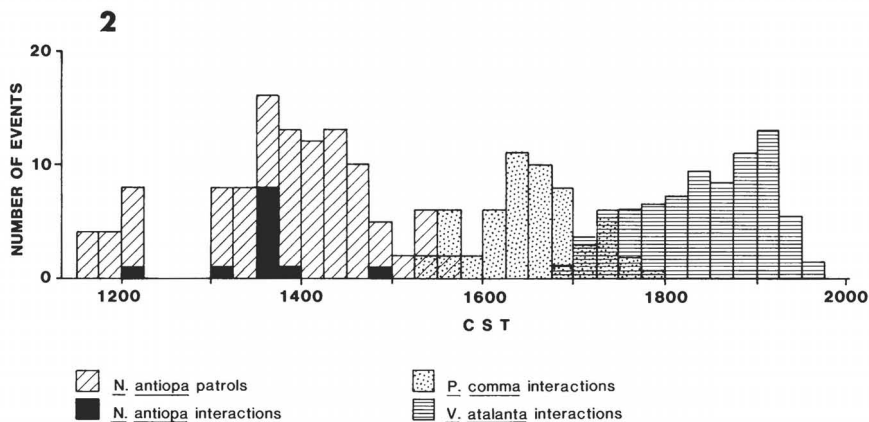
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FIG. 2. Temporal distribution of activity of *N. antiopa*, *P. comma* and *V. atalanta*. *N. antiopa*—total number of patrols and interactions by single occupants for 14, 18, and 21 April 1979. *P. comma*—total number of interactions in a cluster of six perches and nine perches on 21 and 22 April 1979 respectively. *V. atalanta*—mean number of interactions/day for 10 days in mid-June 1979.

trolling. Length of patrols ranged from 2–58 seconds (12.1 ± 9.6 s) (Table 1). Frequency of patrolling was highest between 1315 h and 1445 h (Fig. 2) and was positively correlated with frequency of intruders entering the ravine. Eleven of 12 intractions occurred between 1310 h and 1450 h (Fig. 2). During the four days of observation, seven intruders entered the ravine from varying directions at an intrusion frequency of 0.8/h (7 intrusions in 528 min). The four ravine occupants (one each day) chased the seven intruders 12 times for an interaction frequency of 1.80/h (Table 1). Mean interaction time was 21.2 ± 9.9 s (range 10–40 s) and occupants spent 0.6% (3.2 of 528 min) of their time interacting with intruders.

Intruders entered the ravine flying about 5–6 m above the bottom of the ravine. The occupant flew from his perch, the angle depending upon the intruder's location, to intercept the intruder. After meeting they spiralled together and climbed vertically 10–14 m (Fig. 3). After they leveled off, the occupant chased the intruder around one-half to three-quarters of a circle, 9–15 m in diameter (Fig. 3). When circling, the occupant was usually 30–50 cm behind the intruder. Three to four times during each chase the occupant closed to within a few cm of the intruder. The intruder eventually broke out of the circle and flew out of the ravine (Fig. 3).

Because of the size of the ravine and the tendency for occupants to perch close to one end of the ravine, at times (3 times in 4 days) two
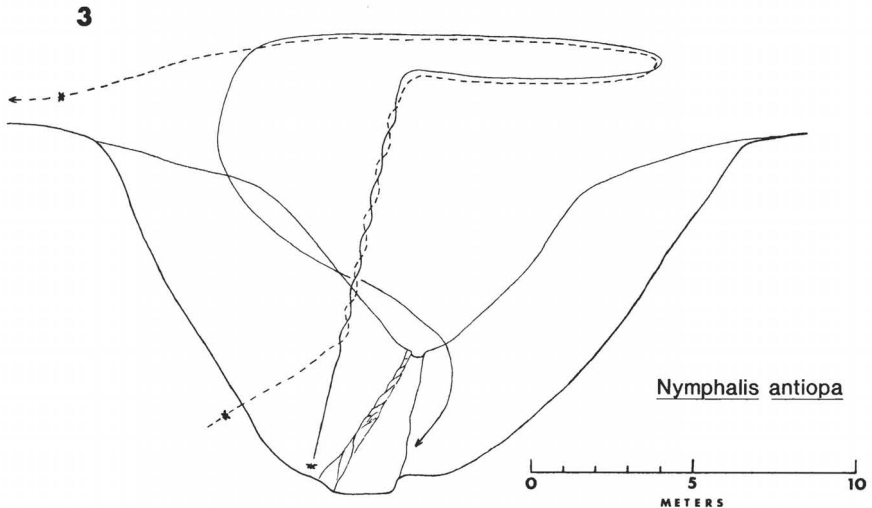
FIG. 3. Flight pattern during typical interaction between two *N. antiopa* males: (——) flight path of territory occupant; (– – –) flight path of intruder.

males temporarily occupied the same ravine. On 18 April the original occupant at the southwest end of the ravine patrolled northeastward and flew through a second male's territory. After six interactions (in 12 min), during which the perching sites of the two males moved northeastward toward the end of the ravine, the original occupant drove the second male out of the ravine. On 21 April the original occupant drove out two different males that temporarily perched in the ravine (Fig. 1). One intruder perched on the side of the northeast end of the ravine at 1323 h. After one interaction at 1341 h he was driven high on the slope, where he set up a small territory. He was observed patrolling and occupying the indicated resting spot at 1402 h. He remained in this new territory for at least 10 minutes, after which observations were concentrated on male #1. The same occupant drove another male out of the ravine after the intruder had perched for two minutes. In this interaction the occupant left his perch and flew about 18 m to the site of the perched intruder. When the intruder rose to meet the occupant, the intruder was driven from the ravine. The occupant apparently had spotted the intruder from his perch and eventually flew to investigate. Occupants also flew to investigate us or light-colored objects placed on a ledge near the bottom of the ravine. On 18 April the occupant flew out eight, 12 and 24 m from his perch to investigate us or the objects on the ledge.

On 14 April 1979 a female entered the ravine from the southwest.

The male intercepted her, and the interaction was similar to a male–male interaction, until they had flown about one-third of a circle. The male prodded the smaller female, who then fluttered her wings twice, three seconds apart, each flutter lasting approximately one second. When she fluttered, the yellow bands on her wing margins were highly visible. After interacting for 20 seconds, the male prodded her downward, and they both dropped into long grass near the top of the ravine. Seven minutes later we found them copulating, and they stayed in copula approximately two hours.

These observations suggest that *N. antiopa* males are unable to determine the sex of an intruder until an interaction is nearly over. By flying behind the intruder and prodding it, the male may be attempting to determine the intruder's sex. If the intruder flips its wings the occupant recognizes it as a female and prods her to drop to the ground. The vertical climb allows the butterflies to rise above the tree canopy to circle.

Besides chasing conspecifics, perching *N. antiopa* males also chased birds and falling leaves. *N. antiopa* is more discriminating than *V. atalanta* (Bitzer & Shaw, op. cit.) when chasing falling leaves. Although the wind blew many leaves into the ravine, the butterflies chased only those which drifted with a rocking motion at approximately the velocity of an intruder. On 8 April 1977 a perching male followed about 30 cm behind one of these leaves and prodded it two or three times before the latter landed on the ground. It is advantageous for a butterfly which perches in early spring not to waste time and energy chasing the large number of fallen leaves which blow about at this time. The butterflies did not discriminate between birds, however, and chased 98% of those which flew over. Their pursuits of birds suggest that *N. antiopa* males can adjust their angle of climb so as to intercept objects passing overhead at different velocities. Birds were chased horizontally until they left the ravine.

Polygonia comma

P. comma males of the Spring brood were observed on 27 March 1978 and 21 and 22 April 1979 in Railroad Park, Ames, Iowa. Males perched on fixed bare spots on the ground or on the sunlit sides of trees about 1–2 m above the ground. They began perching between 1515 h and 1530 h (CST) and left between 1715 h and 1800 h (Fig. 2). Earlier in the day (1200–1500 h) butterflies were seen flying up and down the sides of several ravines in the area.

Like *V. atalanta* (Bitzer & Shaw, op. cit.), *P. comma* males occupied one or a few fixed resting spots (Fig. 4). Unlike *V. atalanta*, they did not consistently outline a fixed territory by patrolling. On 21 April
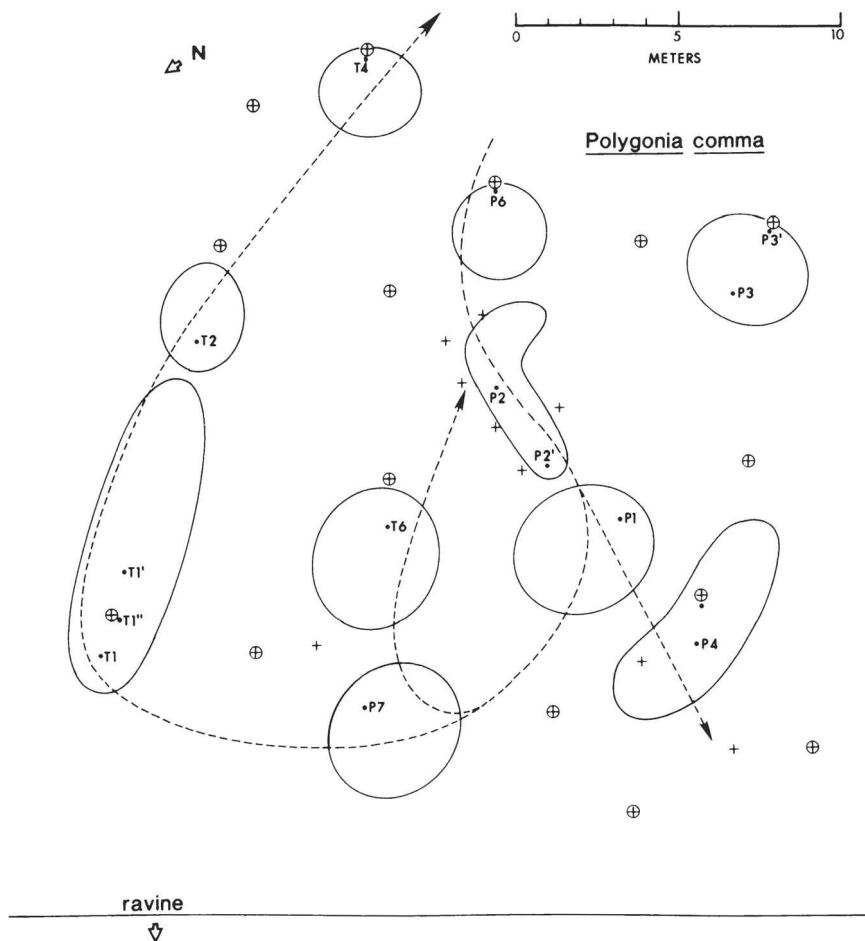
FIG. 4. Territories and perch sites of *P. comma* males on wooded hilltop, 21 and 22 April 1979: (——) areas patrolled by occupants or areas from which intruders chased; (●) perch sites; (⊕) trunk sites of canopy trees; (+) shrubs or 1–2 m saplings; (–––) flight paths of intruders; (Ravine) top of south-east side of ravine in Fig. 1.

only one of the six butterflies patrolled the area around its resting spots (P2, 3 times), while on 22 April four of 10 butterflies patrolled fixed areas (Fig. 4). The areas outlined for the remaining butterflies in Fig. 4 indicate approximate areas from which passing intruders were chased. Butterflies rested on the same spots on 21 and 22 April. After one butterfly displaced another from his perch, the new occu-

pant used the same perch. This suggests that *P. comma* males, like *V. atalanta* (Bitzer & Shaw, op. cit.) choose perches by orienting to certain visual features of the environment, including light-dark contrast.

Intruders always entered from the north-northwest, and the similarity of flight paths suggests that these butterflies navigate along important visual features. On 22 April 18 of 24 patrolling butterflies flew along part or all of one of the three paths shown in Fig. 4, and four intruders went through all territories from P6 through P7 to T4. Although no data were recorded for 21 April (because so many butterflies were interacting simultaneously), most of the intruders passed through P6 and P2 while occupants chased them. Approximately 90% of these intruders continued through P1 and P7, while the remainder flew through P1 and P4 (Fig. 4).

Most interactions occurred between 1615–1645 h (Fig. 2), and the number of interactions varied among perches. Of six perches occupied on 21 April, eight interactions occurred in P1, 13 in P2, one in P3, none in P4, three in P6 and one in P7. These 26 interactions were observed in 87 minutes for a mean frequency of 17.9/h for the cluster of six perches. The greatest frequency for the cluster in a 15 minute period was 36/h between 1615 h and 1630 h. Of nine perches occupied on 22 April, 14 interactions occurred in P2, none in P3, one in P4, one in P6, none in P7, six in T1, one in T2, one in T4, and none in T6. These 24 interactions were observed in 154 minutes, giving a mean frequency of 9.4/h for the cluster. The greatest mean frequency in a 15 minute period was 16/h between 1645 h and 1700 h. The mean interaction frequency per hour per territory was 4.9 ± 4.4 (Table 1). Time of occupancy for sites with the highest frequency of interactions (P1, P2, T1) ranged from 35–115 minutes. Range of occupation for other perches was 0–30 minutes. Perches with the least number of interactions (P3 and P4) were not along the main intrusion routes.

We observed two types of *P. comma* interactions (Fig. 5). In 49 of 50 interactions the occupant dashed up at the intruder, flying about 1–2 m above the ground, and both butterflies spiraled tightly together, rising at a 50–60° angle to a height of 6–8 m in 3–5 seconds (Fig. 5A). Then the occupant began to chase the intruder up a half-circle, 40–50 m in diameter, rising at a shallower angle to 15–30 m. After one butterfly broke out of the circle, the other descended to the resting spot in a twisting path. We timed eight of these interactions, and they ranged from 12–40 seconds ($\bar{x} = 24 \pm 8.8$ s).

In the other type of interaction the occupant intercepted the intruder and both spiraled to a height of about 9 m before levelling off (Fig. 5B). Then one butterfly, 30 cm ahead of the other, dropped
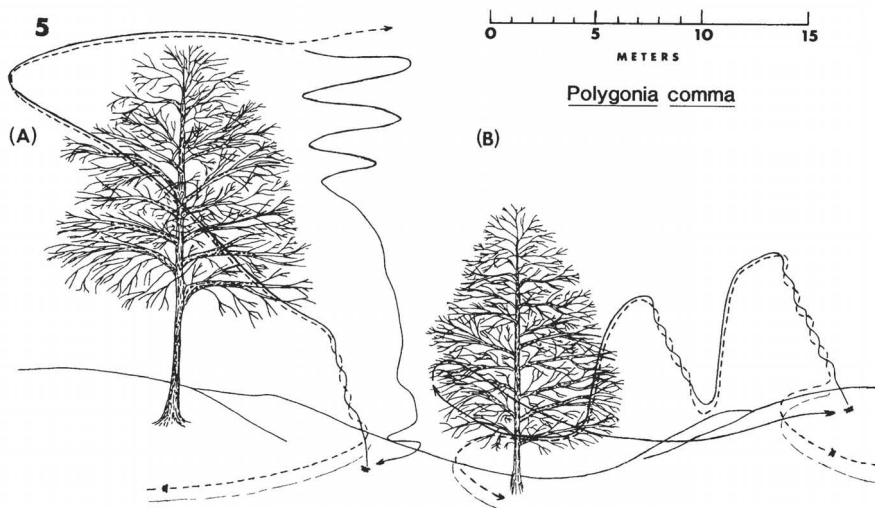
FIG. 5. Flight patterns during interactions of pairs of *P. comma* males: (———) flight path of territorial occupant; (– – –) flight path of intruder. **A,** typical interaction; **B,** single atypical interaction.

abruptly to about 2 m. Again the two spiralled and rose, now to about 6 m, then dropped again, this time just missing the trunk of a large tree. Once past the tree one butterfly chased the other along a straight line until both flew out of sight. Five seconds later and 30 seconds after the intruder had arrived, a butterfly flew back from the direction they had gone and landed on the perch. Baker (op. cit.) observed similar interactions in the nymphalids *Inachis io* (L.) and *Aglais urticae* (L.).

DISCUSSION

Based on Brown's (1975) definition of a territory as a "fixed area from which intruders are excluded by some combination of advertisement . . . , threat and attack," males of *N. antiopa* and *P. comma* occupy territories and exhibit territorial behavior. *N. antiopa* differs from *P. comma* and *V. atalanta* (Bitzer & Shaw, op. cit.) in that the area patrolled is not equivalent to the area defended. The behavior of the above three species is compared in Table 1, which is the basis for the following discussion. The differences among the three species may reflect varying degrees of competition for mating sites and females among the three species.

According to Huxley's (1934) "elastic disc theory," increasing competition for territories should decrease the area which can be successfully defended. *N. antiopa* males roamed over relatively large

areas of the occupied ravine, suggesting that territories were not in short supply. This was supported by the relatively low frequency of intruders and interaction frequencies, as well as the relative ease at which intruders were dislodged. This is in contrast to *V. atalanta* males which had much higher interaction frequencies and occasionally split territories with intruding males (Bitzer & Shaw, op. cit.).

Although they had the lowest interaction frequency, *N. antiopa* shows the highest mean frequency of patrolling. The latter may have been effected by the larger area which they defended and the variety of directions from which females and intruders entered the territories. The relatively large size of *N. antiopa* territories should increase the possibility that a female will fly through (Baker, op. cit.). Continually changing perches also may be correlated with the need to defend such larger territories and to spot potential mates. The relatively small areas patrolled and the shortest mean duration of patrols may be means of countering the energy demands of frequent patrols.

P. comma and *V. atalanta* males probably exhibited lower territory : male ratios (Baker, op. cit.) than *N. antiopa*. There were a greater number of *P. comma* males/unit area, and the territories (=areas patrolled and/or defended) were smaller. Although territories of *V. atalanta* are intermediate in size, there were highly desired or optimal territories that were always occupied night after night and year after year and were reoccupied within five seconds to five minutes after experimental removal of occupants (Bitzer & Shaw, op. cit.). The large number of *P. comma* males per unit area supports competition for territorial sites, but it is difficult to understand why some apparently premium sites (e.g., T1 and P1, Fig. 4) were not occupied both days of observation. The small size of *P. comma* territories apparently negated the need for patrols. There were patrols in only five territories in two days of observation and 17 of 38 patrols occurred in territory T1, the largest territory (Fig. 4).

In addition to greater competition increased compactness of territories and fixity of perch sites also could be effected by increasing tendency for intruders to enter defended areas along specific flight paths. Constancy of flight paths could be the result of at least two factors, prominent visual features and tendency for females to fly through as many male territories as possible. Baker (op. cit.) suggests that the nymphalids *Inachis io* and *Aglais urticae* establish mating territories along visual lines of demarcation, such as hedges, walls and rows of trees. Optimal territories (those most frequently occupied and with the highest frequency of interactions) of *V. atalanta* occurred where sidewalks intersect and near sides of buildings on the Iowa State University campus (Bitzer & Shaw, op. cit.) and along the

tree-lines of forest margins in more natural habitats (Bitzer & Shaw, unpublished observations). Females of polygynous species have greater investment in offspring than males and should be very selective of mates (Trivers, 1972). The opportunity to fly through a number of male territories, possibly two or more times, along a given flight path (Fig. 4) should greatly enhance a female's ability to choose a genetically superior male, possibly expressed by his ability to occupy a highly contested territory, his chasing vigor or endurance, and/or the nature of his aphrodisiac (see discussion of the possibility that males of polygynous insect species have individual "signatures" which females can use to identify them during a testing period; Lloyd, 1981). If females do fly along specific, visually demarcated lines and through as many territories as possible, there should be intense competition for territories along these lines. Non-territorial males would be expected to fly the same paths, assessing, during their flight interactions with territorial males, the feasibility of attempting to displace a territory holder or of establishing a new territory.

When competition is intense males would benefit if they could recognize females early in an interaction. The observation of one male–female interaction suggests that N. antiopa males may not recognize an intruder's sex until late in the interaction (approximately 20 s after the beginning of the interaction). In contrast, V. atalanta males may be able to discern an intruder's sex within five seconds after first encountering an intruder. When interaction frequencies are high and there is an increased risk that another intruder will occupy his territory before he can drive the current intruder way, a V. atalanta male will cut the interaction short after a few seconds of hovering by driving him horizontally to the edge of his territory (Bitzer & Shaw, op. cit.). One suspected male–female interaction supports rapid sex recognition. After a few seconds of hovering with an intruder, the two butterflies dropped downward through a bush (a move not unlike that of the N. antiopa male and female; Bitzer and Shaw, unpublished observations). Unfortunately, an extensive search failed to uncover the pair.

A number of perching species, including some nymphalids, continually change perches, and this has led some investigators to doubt whether any perching butterflies are territorial (Scott, op. cit.). If males change perches this suggests that there is no selective advantage to occupying a fixed perch. N. antiopa males defend areas larger than they patrol; therefore, it is advantageous for them to change perches within the defended area. Since mating territories of many nymphalids are chosen, not for female resources they contain, but because they possess prominent visual markers affecting female flight paths

(Baker, op. cit.; Bitzer & Shaw, op. cit.), lack of prominent visual markers would negate males occupying fixed perches. Shields (op. cit.), in his study of hilltopping species, reported that three species of *Vanessa*, including *V. atalanta*, changed perches frequently. A published photograph of the study area indicates scrub vegetation showing little variation in height and apparent lack of easily differentiated visual lines of demarcation. Scott (op. cit.) reports four species of butterflies with different mate-locating behaviors in different parts of their ranges. Males from different populations of two species chose different topographic features for perching sites; in the other two species, some populations perched while others only patrolled. Whether a species occupies, defends and/or patrols fixed areas may be conditional upon local ecological conditions, such as availability of easily demarcated visual lines, predation pressure, and density of conspecific and interspecific competitors.

If ecological conditions affect fixity of perch sites between species and between populations of the same species, could they affect flight patterns used by occupants to pursue intruders? In our earlier paper (Bitzer & Shaw, op. cit.) we suggested that the vertical spiral helix of *V. atalanta* facilitated the occupant dropping quickly back into his territory to pursue other intruders, while possibly disorienting the intruder in the overhead canopy. In contrast the series of dives and climbs of *I. io* and *A. urticae* (Baker, op. cit.) seem more adapted to driving the intruder up to 200 m from his territory in open country. Baker showed that the distance that intruders are driven from the territory is a compromise between the distance necessary to reduce the chance of the intruder returning and the time required for the owner to return before his territory is occupied by another conspecific. The flight pattern of *N. antiopa* (Fig. 3) appears adapted for driving the intruder to the edge of the ravine and out of sight of the ravine bottom. The two flight patterns of *P. comma* suggest that this species may be able to adapt its flight pattern based upon the nature of the tree canopy and the intensity of competition for perching sites. Forty-nine of 50 occupant–intruder interactions involved driving the intruder above the canopy. However, one interaction was very similar to that of *I. io* and *A. urticae*, which characterize butterflies of more open terrain.

Interspecific competition for perching sites, such as occurs in hilltopping species (Shields, op. cit.), may result in selection for species to mate at different times of the day. Otherwise, perching butterflies would expend considerable energy chasing intruders of other species. Pairs of the three species reported on here may have undergone such selection. The territorial periods of *N. antiopa* and *P. comma* and

those of *P. comma* and *V. atalanta* overlap slightly, i.e., when territorial activities are just beginning or just terminating (Fig. 2). *N. antiopa*'s preference for ravines also may spatially isolate them from *P. comma*. However, one observation emphasizes the importance of temporal isolation between these two species. *N. antiopa* and *P. comma* males occupied the same area on different days, a level area near the top of a ravine.

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