

TERRITORIAL DEFENCE IN THE SPECKLED WOOD BUTTERFLY (*PARARGE AEGERIA*): THE RESIDENT ALWAYS WINS

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Abstract. Males competed for territories, spots of sunlight on the ground layer of woodland, which were the best places for finding females. At any one time only 60% of the males had territories; the remainder patrolled for females up in the tree canopy. Males continually flew down from the canopy and rapidly took over vacant sunspots. However, if the sunspot was already occupied, then the intruder was always driven back by the owner. Experiments showed that this was true even if the owner had been in occupation for only a few seconds. The rule for settling contests was thus 'resident wins, intruder retreats'. Experiments showed that escalated contests only occurred when both contestants 'thought' they were the resident. These results support the theoretical predictions of Maynard Smith & Parker (1976). The reason intruders accept defeat immediately without a serious fight may be that contests are costly and territories abundant.

How should an animal behave in a contest situation if it is to maximize its fitness? The answer is that it all depends on how the other contestants behave. Maynard Smith & Price (1973) have shown that the strategy actually adopted will be an 'evolutionarily stable strategy' or ESS. The ESS is a strategy such that, if all members of a population adopt it, then no mutant strategy can do better.

Most contests in nature are asymmetric (Maynard Smith & Parker 1976). One individual may be more likely to win on account of its greater size (Le Boeuf 1974) or because of a positional advantage (Parker 1974a). Alternatively, the pay-off for victory may be greater to one contestant, for example the owner of a territory who has invested time and energy in its acquisition and defence. Maynard Smith & Parker (1976) show that the ESS is to permit such asymmetries to settle the dispute quickly. Perhaps rather surprisingly, their analysis predicts that this is still the case when the asymmetry is an uncorrelated one, that is to say it is totally irrelevant to the fighting ability of the contestants. Furthermore, they predict that escalated contests will occur only when information about the asymmetry is imperfect.

Despite the vast amount of work on contests in the wild, especially territorial contests, in almost every case the cues used to settle the conflict are unknown. For example, in birds it is often the older individuals that get the best territories (Watson 1967; Krebs 1971) but it is not known why this is so; they may be fitter in some way or simply just first there. To identify the cues an experimental approach is needed

and insect contests provide a better scope for this.

In this paper I will show, by means of some simple field experiments, how territorial contests are settled in a species of butterfly. The results are in accord with the predictions of Maynard Smith & Parker (1976), namely that an apparently irrelevant cue can be used to settle a contest quickly and that only in the absence of such a cue will an escalated contest occur.

General Observations

Survival and Movements

This study was conducted from 25 July to 30 August 1976 in Wytham Woods, near Oxford, England. The speckled wood (*Pararge aegeria*) is a woodland butterfly that has rather a complicated life history (Goddard 1962, 1967). My observations were on adults of the second brood of the year.

I walked along a path through the woods, about 1200 m long, and caught with a small net all the speckled wood butterflies that I saw. Each was individually marked on the upper side of the forewings with spots of 'Magic Marker' coloured paint. The marking procedure took about 15 s and to minimize damage to the butterfly I dabbed the quick-drying paint onto the wings through the mesh of the net so that I did not have to handle the animal at all.

Transects were made daily and at different times of the day, and I plotted the position of each individual on a map. The sexes were easily distinguished, the male having a longer, thinner abdomen and more-pointed wings with smaller cream markings. I marked a total of 291 indivi-

duals. These were mostly males, probably because the males were more easily seen, as they spent most of their time fluttering in patches of sunlight on the ground layer of the wood. Females were much less conspicuous, perhaps because they spent more time at rest amongst the vegetation. On cloudy days, early in the morning, all the speckled woods came down onto the ground and opened their wings to warm up. On one such morning, I counted 45 males and 41 females, and on another I counted 15 males and 16 females. Thus I am confident that the true sex ratio was 1 : 1.

Figure 1 shows that the males were very sedentary and nearly all spent their entire lives within 50 m of where I first marked them. The females, however, moved about much more, and so I did not recapture them as often. Two females moved over 600 m from their place of marking.

Because almost every day was hot and sunny, this being one of the hottest and driest summers

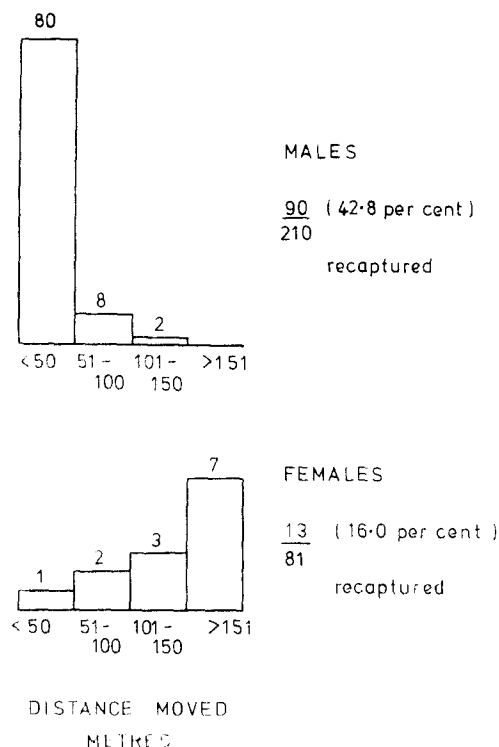


Fig. 1. The distances moved by males and females from their place of marking to that of recapture. For individuals retrapped more than once, the greatest distance moved from the place of first marking has been included.

on record, there was no difference in subsequent survival between individuals marked on different days. Hence I have lumped all the data from different days to calculate the life expectancy. The data refer only to males because I retrapped so few females. From Fig. 2 the average survival from day to day was 86.6%. The average expectancy of further life can be calculated from the formula $(2 - m)/m$, where m is the mortality, in this case 13.4% (Lack 1954, p. 93). This gives a mean life expectancy of 6.9 days. In other words, a speckled wood lives on average for about a week, though as Fig. 2 indicates, a few live for nearly 3 weeks. This calculation assumes that disappearance of the marked individuals was due to mortality and not migration, which seems reasonable considering that the males appeared to be so sedentary.

Behaviour of Males in Sunspots

Speckled woods spent the night high up in the tree tops, 5 to 15 m off the ground. The first signs of activity were seen early in the morning as the warmth of the sun reached the foliage of the woodland canopy. The butterflies opened their wings and orientated towards the sun to warm up. Between 07.00 and 08.00 hours B.S.T. a few could be seen flying about the tree tops and then gradually, over the next hour or two, the males descended to ground level where the sun's rays began to cast pools of sunlight onto the woodland floor. From this time on, throughout the day until early evening, males could be seen fluttering in these sunny pools. It was rare to see any in the shady part of the wood and it seems likely that the sunny spots were preferred because it was here that there was sufficient warmth to enable the butterflies to remain active.

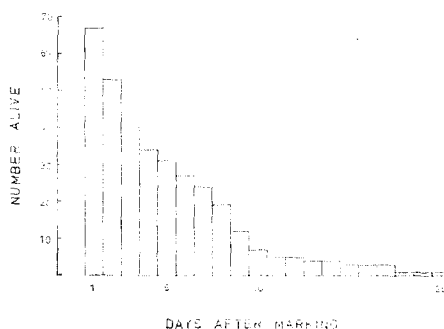


Fig. 2. Survival of individually colour marked males. The number alive on successive days after marking (day 1).

Individual males often spent the entire day in one sunspot. As the sun moved across the sky and the spot moved, they followed it, always keeping within the boundary. During the day males would move up to 50 m in this way as they followed their sunspots' travel across the woodland floor (Fig. 3). They perched on prominent vegetation in the sunspots, usually on a frond of bracken or on a bramble leaf about 1 m from the ground, and flew out to inspect all passing objects. How they behaved towards these objects depended on their identity (Table I). Whenever another male speckled wood flew past, a spiral flight took place. Both individuals fluttered close to each other in mid-air, appearing to bump into each other, and spiralled vertically upwards towards the tree canopy. Then after a few seconds one of them turned and came down again to perch in the sunspot, while the other flew up into the tree canopy.

On the other hand, if the passing object was a female the male's reaction was quite different. He would fly after her, she would often drop to the ground, and then a courtship dance would ensue, very similar to that described by Tinbergen (1972a) for the grayling (*Eumenis semele*). Out of the total of 94 courtships in Table I, 81 were terminated after less than 1 min, on 10 occasions the male pursued the female

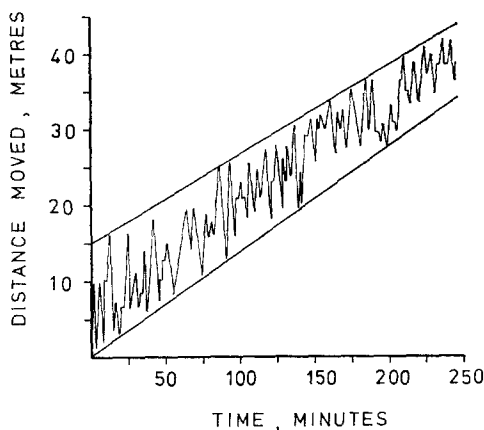


Fig. 3. The behaviour of a territorial male observed continuously for 240 min. The straight lines indicate the boundaries of the sunspot. During the observation period, the sunspot moved a distance of 30 m, as the sun travelled across the sky. It also decreased in size. The continuous zig-zag line indicates flights by the butterfly. For the sake of clarity, the 62 short flights of < 2 m have not been included. Note how the butterfly spends all the time within the sunspot boundary, faithfully following its travel across the woodland floor.

Table I. Behaviour of Males in Sunspots. They Perch on Prominent Vegetation and Sally out to Inspect Passing Objects. How They Behave Depends on the Identity of These Objects

Passing object	No. of occasions		
	Spiral flight	Courtship	Inspect and ignore
Male speckled wood	384	—	—
Female speckled wood	—	94	—
Another species of butterfly*	—	—	66
Another insect†	—	—	35

*Large white (*Pieris brassicae*), small white (*Pieris rapae*), gatekeeper (*Pyronia tithonus*), meadow brown (*Mantola jurtina*), ringlet (*Aphantopus hyperantus*).

†Large Diptera, ladybirds (*Coccinellidae*), wasps (*Vespa*).

into the tree tops where mating probably occurred, and on three occasions I saw the pair fly up into the canopy above the sunspot and engage in copula. Many, perhaps all, of the unsuccessful courtships were with females that had already mated. In 42 out of the 81 unsuccessful courtships, I was able to follow the female and found that she was in the process of egg-laying. There was no male guarding of the female while she was laying so it seems likely that she will not accept further males after she has mated.

Finally, if the passing object was another species of butterfly, or another insect altogether, then the male speckled wood merely ignored it and returned to his perch. Sometimes another species of butterfly landed within a few centimetres, often to feed, yet after the initial inspection it was always ignored.

Figure 4 summarizes the daily activity pattern. It shows that the males occupy the sunspots throughout the day and engage in spiral flights with other males, while the females tend to visit the sunspots later in the day.

Experiments on Territorial Versus Non-territorial Males

Removal Experiments

During the transects it became clear that not all the males occupied sunspots. Many were seen in the tree canopy, 5 to 15 m above the ground. In the middle part of the day I saw 8.6 ± 0.5 sunspot males and 5.2 ± 0.5 canopy males per transect (mean ± 1 SE, $N = 30$, Student's *t*-test, two-tailed, $P < 0.001$). Thus at any one time about 62.3% of the males occupied sunspots while the remainder were up in the tree canopy.

Every now and then, a canopy male would descend to a sunspot below. If it was unoccupied, the male would land in it and remain there. If another male already occupied the sunspot, then a spiral flight occurred and one of them would retreat to the canopy while the other returned to the sunspot.

From these observations, I formed the hypothesis that males were competing for the sunspots and the spiral flights were a means of territorial defence. To test this, I did 20 removal experiments. Every time I removed a territorial male from his sunspot, within a few minutes a replacement male came down from the canopy and took over (Table II). The replacement male then remained in the sunspot and himself engaged in spiral flights with other males that came down from the canopy. This experiment shows that males were indeed competing for occupancy of the sunspots, and males that were not territory owners stayed in the canopy. The fact that territorial males faithfully followed their sunspots as they moved during the day shows that it was the sunspot itself that they were interested in, rather than a specific area of ground vegetation. This was well illustrated on several occasions when a male moved with his sunspot and then later on another male defended a sunspot that had meanwhile appeared in exactly the same area that the first male had been a few hours beforehand.

The next question was; why do males compete for sunspots? Not for food apparently: in over

100 hours' observation I only saw a male feed in his sunspot on two occasions. Both times he licked a bird dropping for about 10 s. In fact the speckled woods appeared to do most of their feeding up in the canopy, where I saw them licking tree buds and leaves. The most likely explanation was that the males competed for sunspots because these were the best places to find females. The observation that after a successful courtship the sunspot male left his territory to mate up in the tree canopy supported this idea.

To see whether a male in a sunspot encountered more females than a male high up in the tree canopy, I sat in a tree, about 7 m from the ground, for 7.5 h. I watched the sunspot below me and at the same time observed a similar area of tree canopy opposite. The sunspot male was marked and so were the canopy males, which I had captured when they came down to intrude into the sunspot. The sunspot male successfully defended his territory throughout the watch, despite the fact that the canopy males were continually coming down to intrude. Each time he appeared to chase them off in a spiral flight. Table III shows that the territory male in the sunspot did indeed encounter far more females than the canopy males. In the absence of better data, I assume that this means that a sunspot male will enjoy more matings per unit searching time than a male in the canopy.

I conclude that the results from this section support the hypothesis that males compete for sunspots because these are the best places for finding females.

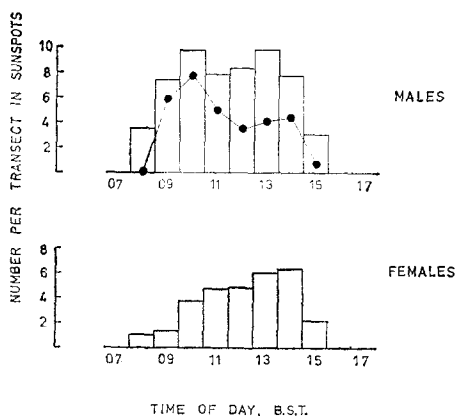


Fig. 4. Diurnal changes in the number of males and females in sunspots on the woodland floor (histograms). The mean number of spiral flights between males in the sunspots is also shown (solid circles). Data from at least six transects at each time of day.

Table II. Removal Experiments. On Every Occasion that a Territory Owner was Removed from his Sunspot, another Male came down from the Canopy above and took over the Territory

No. of occasions the male was replaced	20
No. of occasions the male was not replaced	0
Mean $\pm$ SE time to replacement (min)	3.81 $\pm$ 0.79

Table III. Sunspots Versus the Tree Canopy above. The Number of Females seen in a 7.5-h watch

	Sunspot	Tree canopy
No. of males	1	5
No. of females	22	5
No. of courtships	4	1
No. of courtships per male	4.0	0.2

The Probability of Finding a Territory

Given that not all males occupy sunspot territories at any one time, what is the chance that a canopy male will eventually have his own sunspot? Out of 21 individually marked males which I saw in the role of intruders from the canopy, 19 of them (90.5%) were later seen as territory owners, defending their own sunspots. Five of these were defending territories less than 1 h after I had seen them as intruding canopy males. Four were territory owners 1 to 4 h later, six 1 day later, one 2 days later and three 5 days later. Of course these latter males may well have found territories in between the times I saw them as intruders. Thus there is a very good chance that a male at present an intruder will soon become a territory owner. In fact it is likely that all males, sometime in their lives, defend sunspot territories.

Mate Searching Behaviour

The way the sunspot males and the canopy males searched for females was very different. Sunspot males, as I have described above, remained in a small area and sallied out to inspect passing objects ('perching behaviour'). The canopy males, on the other hand, were continually on the move, flying up and down long stretches of up to 30 m ('patrolling behaviour', Scott 1974). Active patrolling would seem to be an appropriate searching strategy in the canopy where females were scarce, while the 'sit and wait' perching strategy would seem to be a good method of search in the sunspots where females were more abundant and patchily distributed.

Individuals switched rapidly from one searching strategy to another. Early in the morning, before the sunspots had formed on the ground, males actively patrolled in the canopy. Later in the day, the same males were seen showing perching behaviour in the sunspots below.

On cloudy days, when there were no sunspots and yet it was still warm enough for activity, all the males engaged in patrolling behaviour both in the canopy and at ground level. Presumably under these conditions there were no best patches for locating females and so the sit-and-wait strategy of perching and defending a small area was not economical. In support of this idea, males that met each other on cloudy days did not engage in spiral flights but merely turned and flew off in different directions. Out of 36 male: male encounters on cloudy days I

only saw one spiral flight, whereas out of 384 male: male encounters on sunny days in sunspots, there was a spiral flight on every occasion. It could be argued that the males were just too cold to spiral on cloudy days. This is unlikely because they were certainly active enough to court females under these conditions.

The Effect of Sunspot Size on Territorial Defence

Sunspots varied in size, and Fig. 5 shows that the larger the sunspot, the more females visit it. A sunspot of twice the area has approximately twice the number of females. It may be expected therefore that the males should try to defend the largest sunspots they can, because by so doing they will encounter more females.

In small sunspots the resident male can detect all the intruding males that come down from the canopy. His perching behaviour and spiral flights result in him being the sole occupant of the sunspot. However, as the sunspots increase in size, there is an increasing probability that a male will have to share it with a second male. This is because another male is able to land in the sunspot and engage in perching behaviour without detection by the other owner. Thus the maximum area a single male can defend is related to his ability to detect intruders. Still larger sunspots have three or even four males in them simultaneously (Fig. 6). Figure 7 shows that the chance of finding a male in a sunspot is directly related to its area. In other words, just as with the females, there are twice as many males in sunspots of twice the area.

The optimal searching strategy for any one male will depend on what all the other males

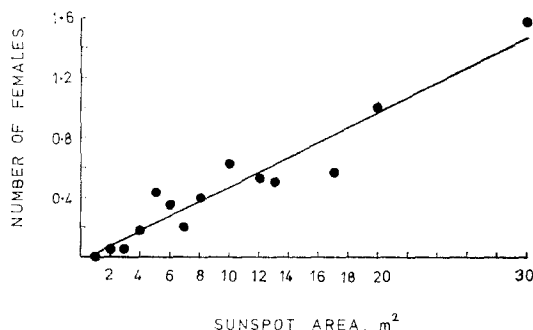


Fig. 5. The number of females seen per transect visit in sunspots of different sizes. Fitted regression line, $y = 0.049x - 0.026$. Correlation coefficient = 0.955, $P < 0.001$.

are doing. For example, if they all went for the large sunspots then it would begin to pay a male to go to the smaller ones. Figure 8 shows that the male searching behaviour is such that the number of females a male will expect to encounter in sunspots of different areas is constant. In other words, the profitability of the large sunspots is the same as that of the small ones because several males have to share the females in large sunspots. Male searching behaviour thus follows an ESS. This is rather like the situation studied by Parker (1974b) where the distribution of male searching behaviour in the dung fly (*Scatophaga stercoraria*) was such that the expected number of matings by males adopting different searching strategies was also equal.

The Cue to Decide Territorial Contests

How do males compete for sunspots? The spiral flights look rather like contests; if so, then how do the contesting males decide who will remain in the sunspot and thus encounter the most females? In this section I will describe some simple experiments whereby I examined these questions. The experiments were all done in small sunspots where a single male could successfully defend the territory. All involved owners and intruders that were individually marked with coloured paint spots.

The first question I asked was, what would happen if I captured a territory owner, allowed an intruder to come down from the canopy and take over, and then released the original owner back onto his territory again? Table IV shows the outcome of this experiment. On 10 occasions,

each in a different sunspot with a different male, I removed the owner and held him in a net. Within a few minutes a replacement male arrived and took over the territory. I allowed the replacement to land in the sunspot and perch there for 10 s. Then I released the original owner back onto the sunspot. The replacement immediately flew over to the owner and the two males engaged in a spiral flight up towards the tree canopy. After a few seconds they parted. One flew up to the canopy and one returned to the sunspot. On all 10 occasions it was the original owner who retreated. One possibility could have been that the owner was suffering from his period of captivity in the net. To control for this, I did another 10 experiments where I held owners in a net for the same length of time as in the previous experiments, and then released them back onto their empty territories. (If an intruder had taken over in the meantime then I

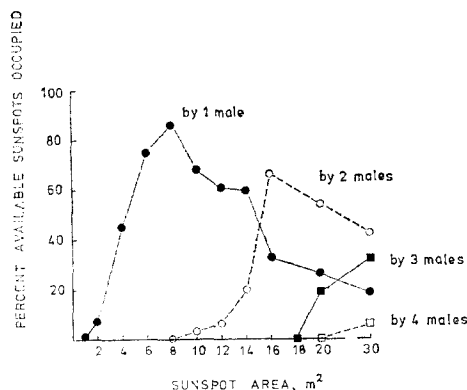


Fig. 6. The percentage of available sunspots of different sizes that were occupied by one, two three or four males simultaneously.

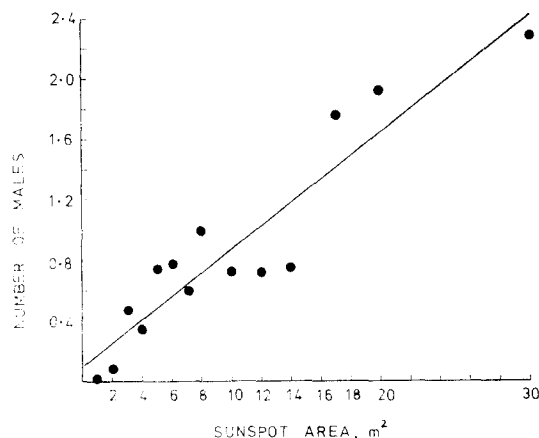


Fig. 7. The number of males per transect visit in sunspots of different sizes. Fitted regression line, $y = 0.077x + 0.110$. Correlation coefficient = 0.934, $P < 0.001$.

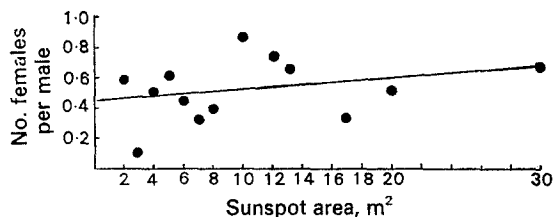


Fig. 8. The number of females a male can expect to encounter in sunspots of different areas. Fitted regression line, $y = 0.008x + 0.442$. Correlation coefficient = 0.307, $P > 0.10$. The slope is not significantly different from zero.

removed it.) On all 10 occasions the owner stayed in the sunspot and continued to defend it.

Although the original owners always lost their territories to the replacements, I thought that at least they would not give in without a good fight. So I compared the duration of the spiral flights between the replacement and the released owner with that of other contests. Table V shows that there were no significant differences. In other words, not only does the original owner lose the contest, he retreats without much argument!

Table IV. Remove and Replace Experiments. When a Territory Owner is Removed from his Sunspot and then Released Again, He Loses His Territory if there is a Replacement Male Present, but Retains it if it is Empty

	No. of occasions the original owner:	
	Retained territory	Lost territory
Replacement present	0	10
No replacement	10	0

These observations strongly suggested that the rule for deciding the territorial disputes was 'resident wins, intruder retreats'. To test this further, I did three experiments each with a pair of males. In the first part of each experiment one male was the resident and the other was the intruder. In the second part, I captured the original owner and allowed the other male to

Table V. Remove and Replace Experiments. When Owners are Released back onto their Territories the Spiral Flight with the Replacement is No Longer in Duration than in Other Situations. (Student's *t*-tests, no Significant Differences)

	Spiral flight duration in seconds	
	Mean $\pm$ 1 SE (no. obs.)	
By original owner before removal versus intruders	4.29 $\pm$ 0.70	(17)
By replacement versus re-released owner	3.07 $\pm$ 0.24	(13)
By replacement versus other intruders	3.86 $\pm$ 0.42	(29)

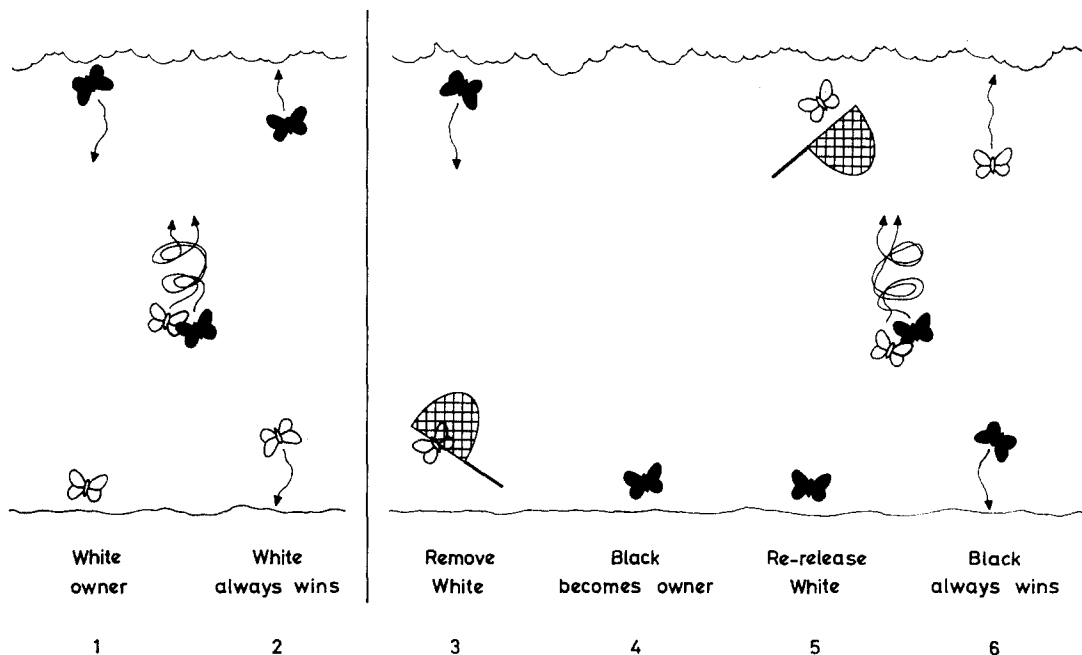


Fig. 9. An experiment which shows that the rule for settling contests for territories in the speckled wood butterfly is 'the resident always wins'. This experiment was done three times, each time in a different territory with a different pair of individually colour marked males. In the figure one male is represented as black and the other as white. Who wins the contest depends on who is the resident. Drawing by Tim Halliday.

take over the territory so that the roles were reversed. On every occasion the resident won the contest, regardless of which male it was (Fig. 9).

Two other observations fit in with the idea that the resident always wins. Out of 210 spiral flights between males where I had the owner marked, it was the owner which won the contest on every occasion. This applied even when the owner was a very tatty male whose wings were torn and the intruder was a perfect male in mint condition. Thus the spiral flights, only a few seconds in duration, cannot be regarded as contests at all. Rather they are a short conventional display where, to put it anthropomorphically, the owner says 'I was first here' and the intruder says 'Sorry, I didn't know there was anyone occupying the sunspot, I'll retreat back to the canopy'.

If the intruder is certain to lose, then why does it bother intruding in the first place? The answer is that it usually doesn't. From the removal experiments, the time for a replacement to take over the territory gives a measure of the rate of intrusion onto empty territories. The rate of intrusion onto occupied territories can be measured by the time between successive spiral flights that the owner makes with intruders. Table VI shows that the rate of intrusion onto occupied territories is only about half that onto unoccupied ones. This suggests that the canopy males can to some extent determine whether the sunspot below them is occupied, probably by detecting the owner flying about below them, and if it is, they don't bother intruding. On some occasions, however, the intruder presumably has to go right down into the sunspot to see if there is an owner present.

Finally, if the contestants for a sunspot use the rule 'resident always wins', then what happens if both of them think they are the resident? To test this, I attempted to release a

second male into an occupied territory without the resident noticing. This was rather difficult to do and on most occasions I failed because the owner spotted the second male before he landed in the sunspot, flew over to him and chased him off with a brief spiral. However, on five occasions I managed to put an intruder onto a territory unnoticed so that two males were perching together in the same sunspot. The first individual to fly was quickly spotted by the other and a spiral flight occurred. Table VII shows that this was over 10 times as long in duration as the normal spirals when the roles of resident and intruder were clear to the contestants. Thus when both males think they are the resident, an escalated contest occurs. From all these experiments, it seems that a male only has to land in a sunspot for a few seconds to regard himself the owner of the territory.

I must emphasize that my experiments were done in small sunspots where there was only room for one male at a time. In large sunspots, as described above, several males reside together. When males that share these large sunspots meet, they do not indulge in escalated contests but spiral briefly, part, and then both return to the sunspot. Thus sunspot size appears to affect the behaviour of two residents when they meet.

Discussion

The Resident Always Wins

My main conclusions are as follows. Males competed for occupancy of sunspots because these were the best places to find females. At any one time only about 60% of the males occupied sunspots; the remainder stayed in the tree canopy. The canopy males continually came down into the sunspots and quickly took over any vacancies, but if the sunspot was already occupied then they always retreated back to the canopy again after a brief spiral flight with the owner. Two experiments showed that the rule for deciding the result of these contests

Table VI. The Rate of Intrusion onto Empty Territories is Greater Than onto Occupied Territories (Student's *t*-test, Two-tailed, $P < 0.05$)

	Time (min)	
	Mean $\pm$ 1 SE	(no. obs.)
Empty territories		
(Time for replacement to arrive)	3.81 $\pm$ 0.79	(20)
Occupied territories		
(Time between successive intrusions)	7.81 $\pm$ 1.02	(57)

Table VII. The Spiral Flight Between Two Males is Much Longer in Duration when Both Regard Themselves as Residents than when the Role of Resident and Intruder is Clear to the Contestants. (Mann-Whitney *U*-test, Two-tailed, $P < 0.001$)

	Spiral flight duration (s)	
	Mean $\pm$ 1 SE	(no. obs.)
Prior ownership cue present	3.65 $\pm$ 0.23	(110)
Prior ownership cue lacking	39.60 $\pm$ 7.35	(5)

was 'resident wins, intruder retreats': (1) Owners removed from their territories, and then released back again, always lost contests with replacements, even if the replacement had only been there for a few seconds. On the other hand, owners released back onto their empty territories always retained them. (2) In contests between pairs of males where the roles of owner and intruder were alternated, the resident always won, regardless of which male it was.

How do contestants know who is the resident and who is the intruder? I think the answer is that a male who has actually landed in the sunspot, even for only a second or two, regards himself as a resident while a male still fluttering in the air and who has not yet landed in the territory, regards himself as an intruder. In all the contests I observed it was the male already perched in the sunspot who won the contest by flying up to intercept a male in flight before it could settle in the territory, and then engaging in a brief spiral contest. When I did the experiment of introducing a second male into an already occupied sunspot, so that both were perched simultaneously in the territory, then an escalated contest occurred, presumably because both males had landed in the sunspot and thus both thought they were the resident.

A similar study has been done by L. E. Gilbert (described in Maynard Smith & Parker 1976). He allowed two males of *Papilio zelicaon* to occupy the same territory (a hilltop) on alternate days keeping them in the dark during their 'days off'. When released together after 2 weeks there was severe escalation rather than the usual conventional settlement where the resident won after a brief 'contest'. Both Gilbert's experiment and mine support the theoretical predictions of Maynard Smith & Parker (1976): the ESS in an asymmetric contest is to permit the asymmetric cue to settle the contest quickly. This applies even when the asymmetry is an uncorrelated one (in our experiments 'first there'), that is to say irrelevant to the fighting ability of the contestants. Escalated contests only occur when information about the asymmetry is not clear to the contestants.

Comparison With Other Contests Where the Resident Does not Always Win

A speckled wood territory owner who leaves his sunspot, even for only a few seconds, has lost it if a replacement takes over in his absence. In contrast, several studies have shown that in other animal contests the territory owners can

leave their territories and then return sometime later and successfully evict replacements (Alexander 1961, crickets; Harris 1970, oystercatchers; Davies 1976, wagtails). Why is there a difference between these studies and the speckled woods? I think there may be two important factors:

(1) In the speckled wood contests, the intruder has a high probability of later owning a territory himself; 90% of intruders were later seen defending territories, some less than 1 h later. In addition, a long contest is probably costly, both in terms of wasted time and energy and also perhaps in the risk of physical injury, such as wing damage during the spiral flights. Given these two facts, we would expect a conventional cue to settle the contest quickly (Maynard Smith & Parker 1976). Indeed, what appears to be 'territorial defence' may simply be the evolutionarily stable strategy due to the asymmetry between the contestants in time of arrival in the sunspots (Dawkins 1976, p. 86).

Now, in the other studies I referred to above, it is possible that the chance of finding another territory is low, so that it is worth the original owner fighting hard to retain his patch of ground. Conversely, it may be worth the intruder's while to fight hard in an attempt to oust territory owners. In these cases the winners of contests may be decided, not by some arbitrary cue such as 'first there wins', but by some cue relating to the resource-holding potential of the contestants (Parker 1974a; Baker 1972).

(2) In these other studies, the territory owners have spent considerable time learning the characteristics of their territories. Thus they are probably better at exploiting the territory's resource than are intruders. For example, in the pied wagtail (*Motacilla alba*) (Davies 1976), the owner has knowledge of the best feeding patches within the territory and he systematically exploits them to allow for resource renewal. Intruders who land in the territory during the owner's absence have no such knowledge and they feed at a lower rate because they waste time exploiting recently depleted food patches (Davies, in preparation). Therefore the 'pay-off' for victory is greater for the territory owner, which may explain why it can leave its territory and then return and successfully evict replacements. In situations such as these, where there is an asymmetry due to the owner's greater knowledge of the territory, it may be expected that if an intruder could occupy the territory for long enough to learn its characteristics, then

the owner would be less likely to win back his territory when he returned. There is some evidence that this is the case (Smith 1968, squirrels; Krebs personal communication, great tits *Parus major*). In this context it is interesting to note that although pied wagtails frequently leave their territories, they never leave them unattended for too long and return at regular intervals in order to evict intruders (Davies 1976).

Now insects are certainly capable of learning spatial cues (Tinbergen 1972b; Collett & Land 1975), so that it seems unlikely that butterflies cannot learn the characteristics of their territories (see Baker 1972). However, the speckled wood's territory is not a fixed area; it is a sunspot that is always on the move. This may mean that an owner is prevented from learning his territory's characteristics because they are continually changing. Unlike the other studies I discussed above, it is possible that the speckled wood sunspot owner is no better at exploiting the territory's resource than is an intruder. Perhaps this is why a temporal cue (first there) is the asymmetry that is used to settle the contests, as opposed to a spatial cue which is used in situations where territory characteristics are learned (Tinbergen 1964, p. 63).

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