



Seasonal polyphenism and leaf mimicry in the comma butterfly

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The comma butterfly, *Polygonia c-album*, exhibits seasonal polyphenism with a darkish winter morph and a lighter summer one. Phylogenetic analysis suggests that the winter morph represents the ancestral condition. We suggest two hypotheses for the evolution of the summer morph and the maintenance of seasonal polyphenism in the comma: (1) that the summer morph is better protected against predation on summer roost sites, whereas the winter morph is better protected on hibernation sites, and (2) that the summer morph is energetically less expensive and results from deallocation of resources from soma (e.g. dark wing pigmentation) to reproduction. We tested the antipredation hypothesis in experiments using great tits, *Parus major*, as predators on winter and summer morph commas presented simultaneously on tree trunks or on nettles. However, this hypothesis was not supported as the winter morph was better protected than the summer morph on both backgrounds. Predation when both morphs were present was lower on nettles, and summer morphs placed in exposed positions on tree trunks outdoors disappeared sooner than winter morphs placed on the same background. In addition, in a final experiment, 18 summer morphs released in their natural habitat in the evening exclusively chose leaves for roost sites, whereas 12 of 19 winter morphs chose a tree trunk, branch or twig. We conclude that evolution of the summer morph is consistent with the life history hypothesis and that its choice of summer roost sites is associated with a low predation pressure.

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The life span of the adult insect is often short as a result of high predation pressure. Although butterflies in temperate areas that start reproduction soon after eclosion usually live for only a week or so, those species that spend the winter as butterflies have an adult life span of some 10–12 months. It is generally true that hibernation represents the stage in which an individual butterfly spends most of its life. Since insects live under high predation pressure, more resources for protection should thus be allocated to the overwintering stage. This expectation appears well supported in butterflies that hibernate as adults, such as the brimstone, *Gonepteryx rhamni*, the peacock, *Inachis io*, and the comma, *Polygonia c-album*, all of which have been described as leaf-mimics (Brakefield et al. 1992). Butterflies are dependent on solar radiation for flight activity, and under sunny conditions can escape from predators by flight once discovered. They often depend on crypsis for survival, however, both during hibernation and during

the active season in the absence of solar radiation. Hence, it is of interest to study predation avoidance of both overwintering and roosting butterflies.

Among butterflies that have more than one generation per year it is not unusual for the different generations to be morphologically different, a phenomenon called seasonal polyphenism. In tropical areas, butterflies typically exhibit different phenotypes during the wet and dry seasons, and satyrine butterflies such as *Bicyclus anynana* appear more cryptic during the dry season and have larger eyespots on the wing in the wet season (Lyytinen et al. 2003). In the northern temperate zone, the satyrine *Pararge aegeria* also exhibits seasonal polyphenism: first-generation butterflies are distinctly different from summer generation butterflies in both colour and body design (Van Dyck & Wiklund 2002). The most extreme form of seasonal polyphenism among temperate butterflies is exhibited by the map butterfly, *Araschnia levana*, in which the spring generation butterflies are red and white, whereas the summer generation butterflies are black and white. The two morphs of *A. levana* also differ in body design (Fric & Konvicka 2002).

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The comma butterfly also exhibits a distinct seasonal polyphenism, in which the overwintering generation has the underside of the wings coloured in various shades of grey to brown, whereas the underside of the wings of the summer generation butterflies (called the *hutchinsoni* morph) are of a much lighter ochreous and fulvous-brown (Frohawk 1924; Ford 1945; Thomas & Lewington 1991). Typically, the winter morph has darker, more melanized, pigments than the summer morph. In tropical areas, the more cryptic appearance of dry season morphs has been explained as an antipredation device, whereas the more accentuated deflective eyespot markings in the wet season forms are thought to confer a selective advantage during the wet season (Lyytinen et al. 2003). However, the adaptive value of seasonal polyphenism among adult butterflies in temperate areas is poorly understood (Gotthard & Nylin 1995). In the family Pieridae, seasonal polyphenism seems to be related to thermoregulation, with the summer generations showing less wing melanization, possibly as an adaptation against overheating (Shapiro 1976; Kingsolver 1995). In the case of *P. c-album*, however, overheating is not considered to be a problem and an adaptive explanation is most likely to be found in a context other than thermoregulatory ability.

To understand the evolution of seasonal polyphenism, it is important to establish which morph represents the ancestral state and which morph is derived (cf. Fric et al. 2004). In *Polygonia*, the greyish brown underside of the winter morph represents the ancestral state (Nylin et al. 2001). Thus, the lighter underside of the summer morph is a derived state in *P. c-album*, and hence, our objective in this study was to understand why the summer generation has evolved a morph with lighter wing pigmentation than the winter generation.

We suggest two hypotheses for seasonal polyphenism in the comma butterfly. The first is based on the idea that the resting sites of comma butterflies vary in colour during the year; as a result the summer morph may be more cryptic in a summer environment, whereas the winter morph may be more cryptic in an autumn/winter environment. The second hypothesis assumes that seasonal polyphenism is a life history adaptation. Because the summer morph commas reproduce without prior diapause, they can allocate more resources to reproduction than the normal overwintering morph, which must allocate more resources to survival prior to reproduction. Hence, the melanic colours of the winter morph, which are likely to be costly to produce (Talloe et al. 2004), are not synthesized by the summer morph commas, which reallocate resources from soma to reproduction. We realize that these hypotheses are not mutually exclusive, and in this study we have attempted to assess their relevance by testing the antipredation (first) hypothesis.

We staged predation experiments in the laboratory in which great tits, *Parus major*, were presented with both comma morphs together on two backgrounds: one large tree trunk representing an overwintering background and one summer background of nettle leaves. Because the birds usually detected the summer morph on the tree trunk first and thereafter detected the winter morph as well (see Results), we also carried out an experiment using

two winter morph commas on the trunk. This was done to test whether the winter morph is less likely to be detected on this background when not accompanied by a summer morph. We also tested late autumn/winter survival of summer and winter morph commas in an outdoor experiment by placing such pairs of butterflies on trunks of old oaks and recording their survival/disappearance. In addition, we tested whether there is a difference in roost site preference between the two morphs. This was done by releasing adults late in the evening during September and observing them until dusk.

METHODS

Study Species

The adults of the winter morph eclose in the middle of summer and feed for a couple of weeks before entering hibernation. Mating and reproduction take place in spring. The first offspring of this overwintered generation have a bivoltine life cycle, whereas the offspring produced later have a univoltine one. The first offspring eclose in early summer and are of the summer morph. These adults mate and reproduce without prior diapause, and their offspring are of the winter morph. Offspring produced by overwintering comma butterflies are also of the hibernating winter morph. Hence, the pool of comma butterflies that mate in the early spring represents both the first and second filial generations of the previous year's overwintering generation.

Knowledge of where commas hibernate is scant, and we have found only four statements in the literature. Frohawk (1924, page 114) stated that the comma 'rests on branches or other supports it may choose, fully exposed'. Ford (1945, page 103) stated that it spends the winter 'exposed on branches or among dead leaves'. Thomas & Lewington (1991, page 134) commented that it relies 'mainly on the dry part of woods, settling low down on elevated tree-roots and other exposed surfaces, in places where drifts of dead leaves will later accumulate to complement their remarkable camouflage'. Finally, Emmet & Heath (1989, page 214) stated that 'Hibernation takes place on tree trunks and branches...'. These statements are in general agreement and, even though the number of commas discovered while in hibernation seems to be low, the fact that they are never found inside unheated attics suggests that they hibernate fully exposed.

General Methods

Offspring from females of *P. c-album* wild-caught in the vicinity of Stockholm, Sweden, were reared on their natural host plant, the stinging nettle, *Urtica dioica*, at 23°C. We produced the winter morph by rearing larvae in a 12-h daylength in an environmental cabinet, and the summer morph by transferring larvae from a 12-h daylength to a 22-h daylength just after they had moulted into the fourth larval instar (cf. Nylin 1989). After eclosion the adult butterflies were released into a flight cage (0.8 × 0.8 × 0.5 m) which was heated and lit by a 400-W mercury vapour lamp. They were fed on 25% sucrose

solution from a sponge that was placed some 10 cm below the top of the cage in a 380-ml plastic jar. The daylength was maintained at 8 h and the winter morph butterflies were taken to hibernation after 2 weeks of foraging. During hibernation, the butterflies were housed individually at 6°C in 150-ml plastic cups sitting on a gauze netting held on to the top of the plastic jar by means of a rubber band. Under these circumstances the commas remained inactive but alive for 6–8 months, and they were taken from hibernation just before the experiments.

Indoor Predation Experiment

The experiments with great tit predators were aimed at testing the relative survival of the two comma morphs on two different backgrounds. They were carried out at Tovetorp Research Station, ca. 100 km south of Stockholm in a room measuring 230 × 240 cm and 195 cm high, and lit by six daylight lamps. In the corners we placed one 2.5-m-high spruce, *Picea abies*, and two wooden sticks 1.90 m high with wooden perches 10 cm long; these wooden perches were almost always used by the birds when consuming the food items. On the floor of the room we placed two longitudinally cut halves of an old trunk of *Salix caprea* 3 m long and about 50 cm in diameter. The halved logs were placed parallel next to each other so that the round outer parts of the trunks were pointing upwards. We maintained the temperature at 11–12°C to decrease the probability that the butterflies would take flight during the trial.

The great tits were caught in cage traps in the vicinity of the Tovetorp Research Station (permit Linköpings djurförsöksetiska nämnd 31–98). Before the trials, the birds spent 2–5 days in separate cages (80 × 40 cm and 60 cm high) with the temperature varying between 15 and 17°C. In these cages, the great tits had access to water, sunflower seeds and suet ad libitum, and a number of mealworms every day. Every cage was also equipped with perches. The birds were all caught, and subsequently released within a week, outside of the breeding season, between mid-December 1999 and the end of February 2000. Each bird was used in one experimental trial only, then ringed and released, near the place where it was originally caught, on the day after the experiment.

Just before releasing a great tit into the experimental room, we placed a pair of comma butterflies either on an autumn/winter background, the tree trunk, or on a summer background consisting of a potted stinging nettle 0.2 m high. On the tree trunk, the butterflies were placed on the deeply serrated bark, approximately 10 cm from each other, with their bodies oriented along the longitudinal rows of bark furrows. On the nettle, the two butterflies were placed on top of two leaves approximately 10 cm from each other and some 10 cm above the rim of the flowerpot. We placed the flowerpot at the head end of the two logs, high enough that the great tit often hopped on to its rim, after hopping along the log and reaching its far end. Approximately 0.2 m from the far end of the log we fastened a petri dish with one mealworm. This was done to help the birds associate the log with food and encourage them to conduct a thorough search for food in

this area of the room. Water was provided in a cup on the floor.

At the start of the trial, a great tit was let into the room through a small hole. Each trial lasted until both butterflies had been consumed or until 30 min had elapsed. Both of us constantly observed the bird from different angles through two one-way windows. We timed all events during the trials with a stopwatch, and noted (1) the time until the mealworm was taken, (2) the time until the first comma butterfly was taken, and (3) the time until the second comma butterfly was taken. After a bird had seized a prey item it would usually fly up to a perch, place the prey item under a tarsus, and start to consume it piece by piece. After eating a butterfly, the bird would wipe its bill against the perch and would then start searching for another food item. We tested 13 great tits with one summer and one winter morph placed on the tree trunk, 14 with two winter morphs on the tree trunk, and 15 with one summer and one winter morph on nettle leaves.

Outdoor Predation Experiment

To assess relative predation on winter versus summer morph comma butterflies, we reared 35 of each morph in the autumn of 1998, and allowed them to feed for 2 weeks in an indoor cage under the conditions described above. After 2 weeks, the butterflies were maintained at 6°C for 2 days. On 13 December we placed 35 pairs, one summer and one winter morph, fully exposed on the bark of 35 oaks, *Quercus robur*, on the campus of Stockholm University. The trees were spread out over an area measuring approximately 1000 × 300 m and were at least 10 m apart. The two butterflies were placed approximately 1.5 m above ground and some 10 cm from each other. We revisited these 35 pairs of butterflies once a day until 17 January 1999, and noted any disappearances. When one or both butterflies had disappeared between visits, we searched the ground beneath the tree for the butterfly or remains thereof, in an attempt to assess whether the butterfly had simply fallen down from its position. We found a butterfly alive on the ground beneath the tree only twice, and we replaced each one in its former position. Comma butterflies generally cease to be active outdoors at the end of August or beginning of September, and the temperatures during the 4 weeks of this study were too low to permit any flight activity. Hence, the butterflies were unlikely to fly away. Although summer morph commas do not normally hibernate, they easily survive for up to 3 months when maintained at 6°C; hence, an eventual difference in disappearance rate of summer versus winter morph commas is unlikely to be caused by a difference in their ability to survive cold weather.

Roost Site Choice Experiment

To assess choice of night roost site, we released comma butterflies on three warm and sunny days in late September 2000 between 1730 and 1900 hours, at Riala 50 km northeast of Stockholm, in an area where commas

are relatively common. Although wild commas are no longer active in the field at this late date, the temperature on these days was high enough to allow flight activity of our released commas that had previously been kept at 25–28°C and natural daylengths for a week in the laboratory. We placed the butterfly on a leaf or stem of an ash, *Fraxinus excelsior*, in a sunny position. After 5–10 min of basking the butterfly would fly away, after which we followed it until it alighted. We watched the butterflies intermittently until 2000 hours to make certain that the position in which they were sitting was in fact the night roost. When planning this experiment, we had hoped to observe the choice of overwintering site, as indicated by the butterfly remaining on the roost site for a longer period; however, no butterfly remained on an observed night roost for more than a single night. In total we identified night roosts for 18 summer and 19 winter morph commas.

RESULTS

Indoor Predation Experiment

All of the comma butterflies that were seized by the birds were subsequently consumed; hence, there is no indication that they were in any sense distasteful to great tits.

The degree of predation differed between the three indoor experiments. When two winter morphs were presented on the tree trunk, most birds did not find the prey at all; when one winter and one summer morph were presented on the trunk, most birds ate both individuals; finally, when both morphs were placed on nettles, about half the birds did not find the prey whereas half of them ate both individuals (Fig. 1). Thus, when a bird had discovered one of the prey items it generally discovered the other one too, and only two birds ate only one of the butterflies. When the commas were presented on the trunk, there were significantly fewer trials with predation when two winter morphs were presented (4/14) than when one winter and one summer morph were presented (12/13; Fisher's exact test: $P = 0.001$). Thus, predation risk was significantly reduced when no summer morph was present. Similarly, when both morphs were presented, there were significantly fewer trials with predation with the nettle background (7/15) than with the trunk background (12/13; Fisher's exact test: $P = 0.013$; Fig. 1). Thus, predation risk was significantly lower when the two morphs were placed on nettle leaves than when placed on a tree trunk.

When both morphs were presented, the birds generally seized the summer morph first (Fig. 2). This was significant when the tree trunk constituted the background (sign test: $Z = 2.60$, $N = 12$, $P = 0.009$) but not in the

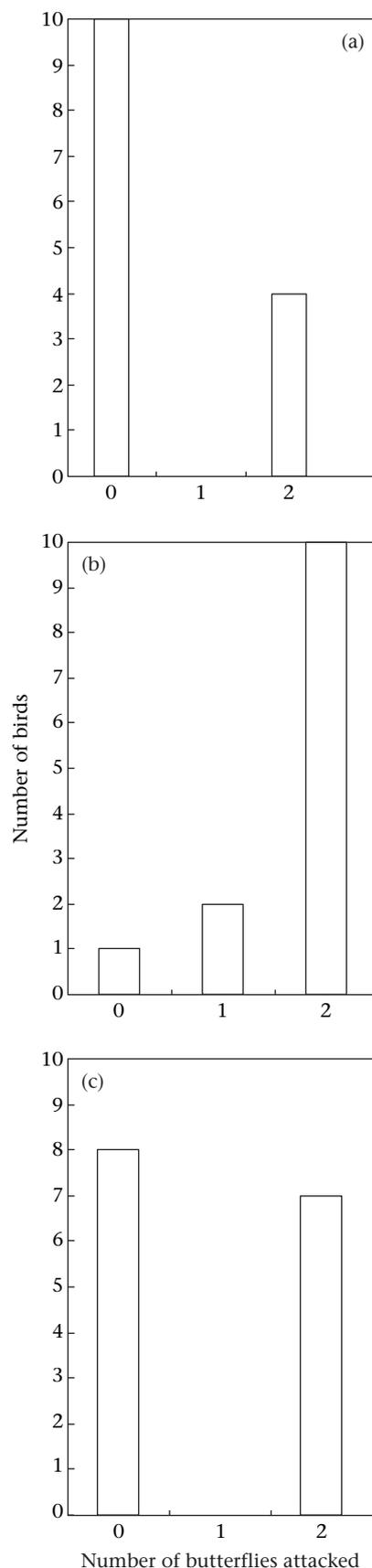


Figure 1. Number of great tits that attacked one, two or no comma butterflies in indoor experiments in which two butterflies were presented in each trial: (a) two winter morph commas on a tree trunk ($N = 14$), (b) one winter morph and one summer morph comma on a tree trunk ($N = 13$), and (c) one winter morph and one summer morph comma on a nettle ($N = 15$). Each bird was used only once and the maximum duration of each trial was 30 min.

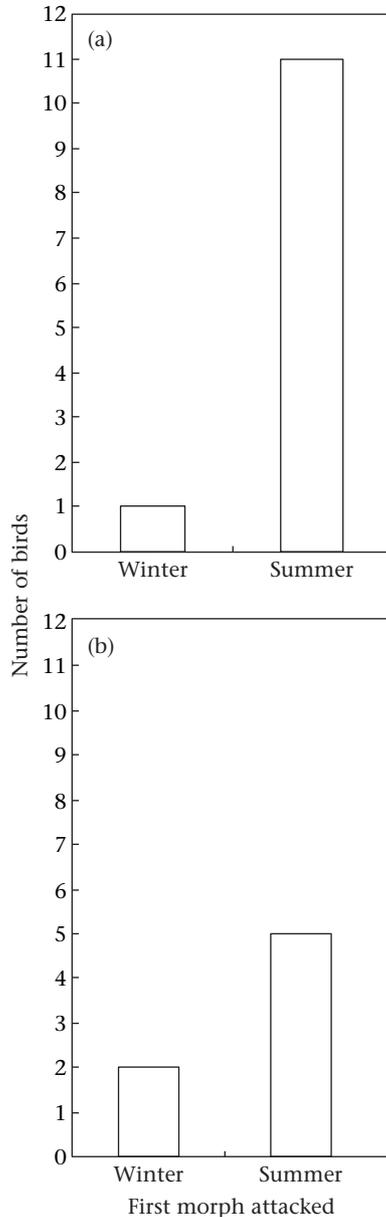


Figure 2. Number of great tits that first attacked a summer morph or a winter morph comma in trials (Fig. 1b, c) in which both morphs were presented simultaneously, on (a) a tree trunk, or (b) a nettle.

experiment with nettles ($Z = 0.76$, $N = 7$, $P = 0.45$). There was no significant difference between the two backgrounds as to which prey was seized first (Fisher's exact test: $P = 0.30$). Taken together, our results show that against the trunk background the winter morph was more protected against predation than the summer morph was, but there is no indication that on the nettles the summer morph was better protected than the winter morph. The type of background was of crucial importance for predation risk on the summer morph. The summer morph was attacked first in five of 15 trials with the nettle background and in 11 of the 14 on the trunk (Fisher's exact test: $P = 0.008$; Fig. 2).

Because all except two birds in the indoor experiments either did not discover any prey item or consumed both

(Fig. 1), it seemed to be the case that, once a comma had been preyed upon, predation on the next one was greatly facilitated. This notion is supported by the finding that the time between the attack on the mealworm (which generally preceded attacks on the commas) and that on the first comma was longer ($\bar{X} \pm SE = 538 \pm 100$ s) than the time elapsed between the attacks on the first and the second comma (202 ± 43 s; paired t test: $t_{20} = 2.80$, $P = 0.011$).

Outdoor Predation Experiment

The comma butterflies that were placed in exposed positions on the tree trunks had a high disappearance rate. Of the 35 pairs of morphs, the summer morph disappeared before the winter morph in 16 cases, and the winter morph disappeared before the summer morph in five (sign test: $Z = 2.18$, $N = 21$, $P = 0.029$). In the remaining 14 instances, both morphs had disappeared 'simultaneously' between census occasions. Summer morph commas had a mean survival duration of 3.3 ± 0.4 days, whereas the winter morph commas had a significantly longer survival duration of 6.8 ± 1.5 days (Wilcoxon signed-ranks test: $Z = 2.76$, $N = 35$, $P = 0.006$). We did not observe any actual cases of predation, but one day after the start of the experiment a group of nuthatches, *Sitta europaea*, were discovered in an area where 10 of the comma pairs were positioned; on the following day not a single butterfly remained, providing circumstantial evidence that these birds were responsible for the disappearance of at least some of the butterflies.

Roost Site Choice Experiment

All of the 18 summer morph commas selected leaves for roost sites, whereas only seven of 19 winter morph commas roosted on leaves and 12 selected a tree trunk, branch or twig for a roost site, a difference that is statistically significant (Fisher's exact test: $P < 0.001$). The green leaves chosen as roost sites by summer morph commas were leaves of ash, *Fraxinus excelsior* ($N = 9$), lilac, *Syringa vulgaris* ($N = 7$), and *Lonicera periclymenum* ($N = 1$) and *Cirsium arvense* ($N = 1$). The winter morph commas also chose lilac leaves ($N = 3$) and ash leaves ($N = 1$) but also leaves of cherry, *Prunus avium* ($N = 2$) and birch, *Betula alba* ($N = 1$). The rest chose roost sites on trunks and twigs of ash ($N = 5$), lilac ($N = 3$), cherry ($N = 2$) and oak ($N = 1$) and a brown winter spike of the grass *Agropyron repens* ($N = 1$).

DISCUSSION

The indoor experiments showed that summer morph commas were less protected than winter morph commas on both the tree trunk (winter background) and the nettle leaves (summer background), but significantly so only on the tree trunk. Thus, on the most likely natural background for overwintering commas, we conclude that the ancestral winter morph is better protected against predation than the summer morph.

The antipredation hypothesis predicts that, apart from the winter morph being better protected against its

background, the summer morph should be better protected against a summer background of leaves; this was not supported in our experiments. The result yields support for the alternative hypothesis that the seasonal polyphenism is a life history adaptation; the lighter coloration of the summer morph could result from greater allocation of resources to reproduction and the associated deinvestment in costly wing pigments. In line with this explanation, a recent study on the cost of melanization in the speckled wood butterfly, *Pararge aegeria*, has indeed shown that the synthesis of this dark pigment polymer comes at a substantial physiological cost (Talloen et al. 2004). Previously, Karlsson & Wickman (1989) have shown that summer morph commas, which reproduce directly without prior diapause, allocate more energy and materials to reproduction than do winter morph commas which allocate relatively more energy and materials to soma. This finding makes sense in a life history perspective that animals that are going to live for a long time need to be built to last. According to this scenario, the winter morph is better adapted to autumn/winter conditions and designed for a longer life span, which is supported by both our indoor and outdoor experiments. For the summer morph, allocation of energy and materials into soma equal to that of the winter morph, including wing pigmentation, would be excessive and allocation to reproduction should have a higher fitness payoff.

We found that the seasonal polyphenism includes a behavioural difference in roost site preference as well as a morphological difference. Thus, summer morph individuals exclusively selected leaves, whereas the majority of the winter morph individuals chose bark structures for roost sites. This behaviour of the summer morph fits well with the finding in the indoor experiments that the summer morph was better protected against predation on the nettle than on the tree trunk background, and has probably evolved to reduce the cost of the lighter coloration. In fact, the behaviour could be the decisive factor making possible the switch to a less costly, and perhaps less convincing, mimetic resemblance in the short-lived summer morph. Because this shift in roosting/overwintering site choice appears to be important for the effectiveness of their defence against predators, further observations are needed to see whether such a change also occurs in the field among wild commas. The reason why the summer morph appears to be more effective in thwarting predator investigation on leaves than on tree trunks might simply be that when leaves are abundant, as in the summer in nature, or as on a whole nettle plant in our experiment, a bird is less likely to investigate leaf-like objects than in the winter when leaves are scarcer in nature, or on the tree trunk in our experiment.

This brings us to the issue of how great tits might perceive comma butterflies. Crypsis is often referred to as a general resemblance to the background, but Cott (1940) made a distinction between general resemblance and specific resemblance to a particular part of the background such as a leaf or a twig (cf. discussion in Brakefield et al. 1992). Specific resemblance is regarded as mimicry by some researchers but not by others (Endler 1981; Rothschild 1981; Pasteur 1982). We contend that the

decisive issue in this discussion is whether or not an element of deception is involved; when a predator mistakes an insect for a leaf, it is clearly deceived but when the coloration and outline of an insect blend so well with its natural surroundings that the predator does not see it, no deception is involved. Thus, general resemblance aims to decrease detection risk whereas specific resemblance aims to decrease recognition risk, giving a prey animal the appearance of an inedible object, thereby making specific resemblance coloration functionally similar to mimicry in the strict sense.

Admittedly, it is often difficult to draw the distinction between these two functions, which rely on the predator's perception and information processing. However, two lines of evidence support our contention that the great tits were deceived by the comma butterflies into believing that they were in fact leaves. First, the time between the bird's attack on the mealworm and its attack on the first comma was significantly longer than the time between attacks on the first and the second comma. This suggests to us that the birds had earlier perceived the presence of the butterflies but had deemed them uninteresting as food objects until they had been discovered to constitute food. Alternative hypotheses are that once a comma butterfly had been consumed, the birds developed a search image which greatly facilitated discovery of the second comma, or that the birds simply returned to the place where they had found the first butterfly and therefore quickly happened to discover the second one. However, we favour the mnemonic interpretation because in some cases the birds seized the second butterfly only a few seconds after having eaten the first, and their goal-directed behaviour gave the impression of returning to a preconceived particular place where they remembered having seen an object similar in appearance to the prey that they had just consumed. Second, we repeatedly observed great tits approaching comma butterflies, especially when the butterflies were sitting on nettle leaves, leaning towards them as if to seize the butterfly but withdrawing at the last instant without actually doing so. This behaviour suggests two things: the approach of the bird demonstrates that the butterfly's leaf-like appearance is not perfect, whereas the withdrawal of the bird demonstrates that it is often sufficiently deceptive.

In summary, we contend that the seasonal polyphenism of the comma butterfly has evolved, not as an antipredator adaptation, but more likely as a result of the benefit conferred upon directly developing butterflies that can reallocate resources from soma to reproduction and in so doing deinvest in soma and cryptic coloration. This is probably facilitated by the lower risk of discovery for the summer morph when selecting leaves for roost sites, in conjunction with a lower selection pressure on excellence in leaf mimicry during the shorter life span of a butterfly that reproduces directly without prior diapause.

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