

Arboreal ants build traps to capture prey

Tiny ants construct an elaborate ambush to immobilize and kill much larger insects.

To meet their need for nitrogen in the restricted foraging environment provided by their host plants, some arboreal ants deploy group ambush tactics in order to capture flying and jumping prey that might otherwise escape^{1–4}. Here we show that the ant *Allomerus decemarticulatus* uses hair from the host plant's stem, which it cuts and binds together with a purpose-grown fungal mycelium, to build a spongy 'galleried' platform for trapping much larger insects. Ants beneath the platform reach through the holes and immobilize the prey, which is then stretched, transported and carved up by a swarm of nestmates. To our knowledge, the collective creation of a trap as a predatory strategy has not been described before in ants.

Allomerus decemarticulatus (Myrmicinae) is specifically associated with the Amazonian ant-plant *Hirtella physophora* (Chrysobalanaceae), which houses colonies in leaf pouches. Workers build galleried structures on their host plant's stems in which they pierce numerous holes that are slightly larger in diameter than their heads, allowing them to enter and exit⁵ (Fig. 1a). First, they cut plant hairs (trichomes) along the stems, clearing a path. Then, using uncut trichomes as pillars, they build the gallery's vault by binding cut trichomes together with a compound that they regurgitate (for details, see supplementary information). Later, this structure is reinforced by the mycelium of a complex of sooty-mould species that has been manipulated by the ants. Fungal growth starts around the holes and then spreads rapidly to the rest of the structure.

We noted that the stems of 34 young seedlings, which had not yet developed leaf pouches, did not bear fungus; nine saplings raised in a greenhouse in the absence of *Allomerus* developed leaf pouches but never bore fungus. However, 15 saplings raised in the presence of ants bore mycelia, whose development was limited to the galleries. When we eliminated the associated ants from five of the 15, the fungus on the galleries grew into a disorganized structure, and none of the nine new stems that developed bore any fungus at all.

Because prey seemed to be immobilized on the top surface of these galleries, we investigated whether these structures could be acting as a trap. Our observations revealed that *Allomerus* workers hide in the galleries with their heads just under the holes, mandibles wide open, seemingly waiting for an insect to land. To kill the insect, they grasp its free legs, antennae or wings, and move in and out of holes in opposite directions until

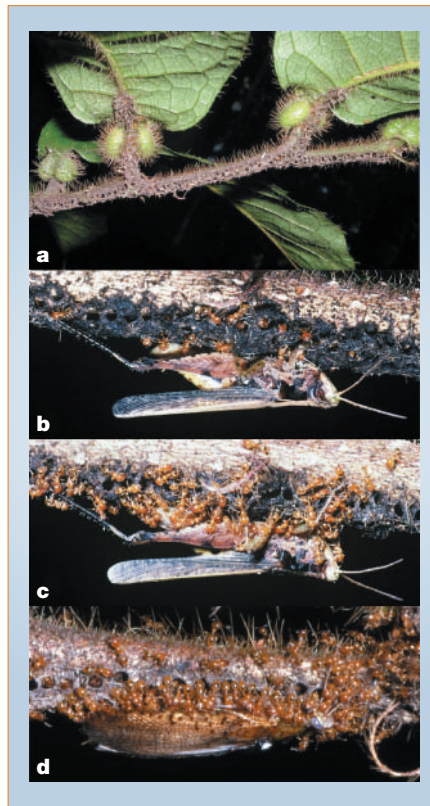


Figure 1 Galleried platforms built by *Allomerus* workers act as traps for prey. **a**, Base of the lamina of two *Hirtella physophora* leaves: the pouches serve as ant nests, which are interconnected by a gallery pierced with numerous holes. **b**, Start of the capture of a locust. **c**, One hour later, recruited workers have left the gallery in order to bite, sting and stretch the prey. **d**, Completion of a cricket capture.

the prey is progressively stretched against the gallery and swarms of workers can sting it (Fig. 1b–d). The ants then slide the prey over the top of the gallery — again moving in and out of holes, but this time in the same direction. They move it slowly towards a leaf pouch, where they carve it up.

Because the requirement for protein is crucial, some arboreal ants consume parts of the Hemiptera that they attend⁶, others rely on microsymbionts to recycle nitrogen⁷, and some have a thin cuticle and non-proteinaceous venom that economizes on nitrogen use⁸. Nevertheless, most of them must capture prey that land on their host plant³. Given this constraint, the tiny *A. decemarticulatus* workers have developed a tripartite association with their host plant and a fungus collectively to ambush their prey.

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Predation

Prey plumage adaptation against falcon attack

Several plumage types are found in feral pigeons (*Columba livia*), but one type imparts a clear survival advantage during attacks by the swiftest of all predators — the peregrine falcon (*Falco peregrinus*)^{1,2}. Here we use quantitative field observations and experiments to demonstrate both the selective nature of the falcon's choice of prey and the effect of plumage coloration on the survival of feral pigeons. This plumage colour is an independently heritable trait³ that is likely to be an antipredator adaptation against high-speed attacks in open air space.

The polymorphic feral pigeon is ideal for investigating the effects of different plumage combinations on predator success. One plumage phenotype — known as the 'wild' variant — is blue-grey but has a white rump between the base of the tail and the lower back, closely resembling the feral pigeon's rock-dove ancestor^{3,4} (Fig. 1); all other plumage types lack this contrasting rump patch³. We tested whether the wild coloration might impart a selective advantage over other plumage types during high-speed diving attacks by falcons, which often exceed 157 m s⁻¹ (ref. 2; Fig. 1a).

During a seven-year period, we recorded 1,485 attacks by five adult peregrine falcons on free-ranging flocks of feral pigeons in Davis, California, during their daily linear

commute, and an additional 309 attacks when three of these falcons were juveniles. For each attack, we noted the plumage phenotype of the selected pigeon and whether the stoop led to a successful capture (for methods, see supplementary information).

To determine the natural distribution of plumage phenotypes, we banded and recorded data from 5,235 pigeons in the study area. Adult falcons selected plumage phenotypes for attack in the same relative proportions that occurred naturally (Fig. 1a, inset), except for the wild phenotype ($P=0.006$). Juvenile falcons, however, attacked all plumage phenotypes in proportion to their frequency in the population.

Comparison of adult and juvenile falcons revealed a significant difference in the plumage phenotypes they selected as prey ($F[5,1782]=2.129$, $P=0.05$; Fig. 1b). But there was no difference between adults and juveniles in their captured pigeons' pattern of plumage ($F[5,585]=0.39$, $P=0.85$; Fig. 1b), suggesting that both age classes learn to avoid the wild plumage during attacks.

Adults were significantly more adept hunters, capturing their prey on 40% of stoops, whereas juvenile success was only 19% ($P=0.0001$). Both adults and juveniles, however, showed a significant interaction between the phenotypes selected for attack and those captured (adult: $F[5,2075]=233.7$, $P=0.0001$; juvenile: $F[5,360]=2.66$, $P=0.02$; Fig. 1b). Much of this effect was driven by the wild phenotype, which accounted for only 2% of all captures in both age classes.

To confirm the advantage afforded by a white rump to pigeons during a high-speed attack, we captured 756 wild and blue-barred pigeons and switched their rump-patch feathers. We then released these pigeons and monitored predation by three adult peregrine falcons. After plumage transfer, we found that capture rates were reversed (Fig. 1c). The original wild phenotype now suffered predation at the same rate as the unmanipulated blue-barred type, whereas the manipulated blue-barred type now had rates of predation as low as the unmanipulated wild type ($P<0.0001$). This indicates that the dorsal white rump patch is important for the survival of feral pigeons during attacks by peregrine falcons.

All feral pigeons perform the same evasive roll during predation by falcons (Fig. 1a). The protective white patch may disguise the initiation of the pigeon's evasive roll by contrasting conspicuous (white patch) and cryptic targets (grey wings and body)⁵. A fast-flying falcon primed to a conspicuous target centered on the roll might fail to detect the dodge initiated by the cryptic wings as the predator closes from behind. When pursued by predators, schools of fish in open water and many shorebirds also display their dark dorsal and light ventral surfaces in a display that alternates between a cryptic and a

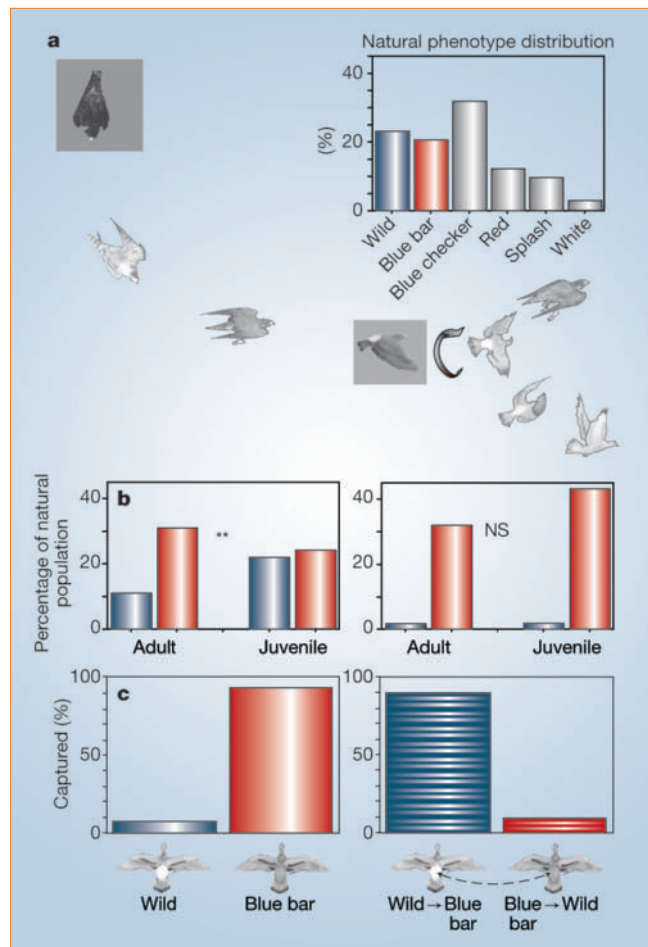


Figure 1 Adaptive coloration in pigeons hunted by peregrine falcons. **a**, Sequence of attack by a falcon as it closes on a pigeon: from the bottom of its dive (top left), the falcon arcs behind the pigeon to begin its 20–100-m horizontal approach; the pigeon then takes avoiding action by dipping one wing, rapidly rotating (arrow), and rolling out of the path of the falcon. Inset, natural distribution of the six pigeon plumage phenotypes in the study population ($n=5,235$). **b**, Percentage of wild-coloured (shown in blue) and blue-barred (shown in red) pigeons selected for attack (left panel) and actually captured (right panel) from the natural population by adult and juvenile falcons. (Statistics indicate comparison of all phenotypes.) **c**, Percentage of wild-coloured (white rump) and blue-barred pigeons captured in the natural population (left panel; $n=203$) and after plumage transfer (right panel; $n=69$) in a field experiment.

conspicuous signal^{6–9}. The use of contrasting patterns as an antipredator mechanism is widespread and may represent a case of convergent evolution.

Given such a selective advantage, why is the wild phenotype not better represented in flocks of feral pigeons? Unlike their monomorphic ancestor, the rock dove, feral pigeons often choose mates with plumage unlike their own (negative assortative mating), and this maintains plumage polymorphisms³. Also, the conspicuous white rump patch could prove disadvantageous when the bird is near cover, such as trees, or confronted by other predators, particularly accipiters and falcons that typically chase down their prey at lower speeds.

In the eastern part of the pigeon's native range in Eurasia, *C. livia* is sympatric with a subgenus of falcons, *Hierfalco*, that typically chase their prey in level flight. Pigeons from this region lack the white rump patch^{1,4}. The decline in recent decades of peregrine-falcon populations worldwide relaxed their selective pressure on feral pigeons, but this has now reversed, with falcons recolonizing many of their former haunts¹⁰. Over the study period, the proportion of wild plumage types in our study population increased significantly relative to blue-barred types ($P=0.01$), in parallel with a steady increase in predation by peregrine falcons. This suggests that, although

pigeon plumage polymorphism persists, falcon predation pressure can lead to an increase in the relative proportion of the wild pigeon phenotype.

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