

Avian resource defence against an insect competitor and a cognition problem*

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Abstract. An account is given on the defence of a food resource by a male of the partially nectar-feeding orange-bellied flowerpecker (*Dicaeum trigonostigma australe*) against the globally biggest carpenter bee (*Xylocopa latipes*) on Panay Isld., Philippines. In the process, the first involving an Old World bird being at the same time a passerine, the bird attacked the bee physically while it was feeding on the ball-shaped (globose) inflorescences of the tree *Nauclea orientalis* (Rubiaceae) also exploited by the defending male and a nearby female. In addition, the defender chased the bee in flight, thus preventing it from landing on the flowers for feeding. The female remained indifferent to the bee, even feeding beside it on the same flower. By contrast, in five years of field work, widely cruising carpenter bees, *X. cuernosensis* included, have never a bee being seen attacked by any bird so that the aggression reported is regarded as food resource defence. The underlying cognitive achievement is best understood by assuming an intruder 'action-based' threat recognition rather than an intruder 'identity-based' threat recognition. Birds, and also fish, are endowed with highly sophisticated 'identity-based' powers of identification of syntopic species and have been shown to recall the community composed of them. However, it is only through an 'action-based' model of cognition

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that birds and fish are thought to utilize the knowledge underlying a species-specific resource defence. An innate ‘identity-based’ object recognition for select community members including predators is known to exist in many cases, but it would probably not accrue the necessary flexibility to resource defence tailored species-specifically to hundreds of species arthropod nectarivores included; as such defence is known to be cutting even across animal phyla and thus exacerbating the cognitive problem for the defender if based on an intruder ‘identity-based’ recognition. – Arguments are presented in support of the idea that the observed resource defence is adaptive, thereby rejecting the ‘mistaken identity’ hypothesis of interspecific territoriality.

Keywords: Resource defence, bird, insect, cognition, interspecific competition, Philippines

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Introduction

Interspecific competition for vital resources is pervasive and can take on a variety of expressions. With an overlap in feeding niches and on an ecological time scale, contest competition is most common and in its extreme form, scramble competition, can have a fatal outcome for one of the competitors (BEGON et al. 2006). The contest may result in members of the competitor species killing each other for food (‘mutual antagonism’) (BEGON et al. 2006, p. 239). In some of the large carnivores foraging benefits the superior when killing the victim without eating it, thereby removing a food competitor (CURIO 1976). Aside from such Victorian ‘claw and fang’ action, interspecific competition can come in many other and less bloody guises, e. g., driving away the competitor from a contested resource including deceit. For example, certain members of mixed species groups ‘cry wolf’ by uttering a predator alarm call to preempt a prey to the caller’s benefit (MUNN 1986, MØLLER 1988, WHEELER 2011). The plethora of behavioural interactions mitigating competition involve cognitive achievements that have come into focus of behavioural ecology (SHETTLEWORTH 2010). For example, EBERSOLE (1977) demonstrated in a small coral fish (*Eupomacentrus leucostictus*) its amazing ability of discriminating between 41 highly diverse, syntopic fish species of potential harm; food competitors were chased away from the territory at a distance increasing with growing overlap in diet whilst predators of the eggs guarded by the territorial male were attacked at still longer distances (see also HARRINGTON and LOSEY 1990; NAKANO and NAGOSHI 1990). This intruder species-specific graded aggression

was later shown to consist of both a 'spatial commitment' and graded aggression tailored to the ecological significance of the intruder in *Eupomacentrus planifrons* (MYRBERG JR and THRESHER 1974; THRESHER 1976). The underlying cognitive mechanisms await experimental elucidation (but see Discussion). Similar results have been obtained for syntopic territorial birds (CORDERO and SENAR 1990), cutting even across oscine families (REED 1982).

Interactions such as these occur usually among community members within the same larger taxon (class and lower). Here I report on a noteworthy episode of competition for food between a small songbird and its hymenopteran competitor, thus also falsifying a causal hypothesis interpreting interspecific territoriality as 'mistaken identity' (MURRAY JR 1971). The alleged 'mistake' would cut across animal phyla.

Observation

The setting.—The episode took place on top of a small ridge overseeing second growth forest from a height of 8m, 100m north of Research Station 'Sibaliw' (11°49'N, 121°58'E), at an elevation of 450m a.s.l. in the NW Panay Peninsula. In the dry 'summer' season, there was bright sunshine on 8 March 2008. The food source contested were flowers of a sparsely blooming *Nauclea orientalis* (Rubiaceae) tree at a height of about 12 m. The habitat was 34 year old second growth forest with few trees of this species. The 'flowers' are ball-shaped (globose) inflorescences of about 4cm in diameter (cf. Fig.1).

The competitors.—They were an orange-bellied flowerpecker (*Dicaeum trigonostigma australe*) male and female and the globally largest carpenter bee (*Xylocopa latipes*) ([HTTP://VESPA-BICOLOR.NET/MAIN/SOLITARY-BEES/XYLOCOPA-LATIPES.HTM](http://vespa-bicolor.net/main/solitary-bees/xylocopa-latipes.htm)), and by default the largest bee (Apidae), too. This is one of 400 species of Xylocopinae (Minkley 1998), and one of two *Xylocopa* species on Panay including *X. cuernosensis*. *X. latipes* is 3.5cm long and, by comparison with the flowerpeckers, was estimated in the field to be 4cm long. It has a very wide distribution in the oriental region. It could not be discerned whether the bee observed was a male that features an exquisitely large brush of smooth hairs at each front leg ([HTTP://VESPA-BICOLOR.NET/MAIN/SOLITARY-BEES/XYLOCOPA-LATIPES.HTM](http://vespa-bicolor.net/main/solitary-bees/xylocopa-latipes.htm)). In India, *X. latipes* and other carpenter bees are important pollinators of many plant species (SOLOMON RAJU & RAO 2006). Specimens, different from that in the present account, were identified later on by G. Hölzler (Vienna). - The birds were easily identified by their plumage characters.

The episode.— It was already ongoing at 4 p.m. when I started the observation and ended 25 min later with the disappearance of the carpenter bee. The male visited

alternatingly one of three flowers two of which were close to each other with the third being 0.5m away. Between visits of a few seconds each the male stayed a few meters distant in the crown. The female also visited the same three flowers and then rested either half a meter away from the last visited or in a neighbouring tree.

When the bee had settled on one of the flowers for feeding the male puffed it on the back and thus made it flee. When the bee approached the flowers anew the male flew toward the bee from behind without making contact when it was still 1-2 m away from the flowers. This made the bee flee even farther away and out of sight. Due to its superior maneuverability and speed the bird could have easily hit the bee. – Once the bee succeeded in landing on one side of the flower ball whilst the female was clinging to it on the other side fully tolerant of the bee. The male then chased the bee away by pecking onto its back as before. During the whole episode there had been three attacks by the male in mid air and two puffing the bee in situ from behind.

The inflorescences with their radially arranged tube-like florets featured a few ‘emergent’ florets sticking out from all the others though this did not much impair the ball-shaped appearance of the flower by large. The ‘emergents’ also had a wider corolla. When feeding, the flowerpeckers poked their bills into the mass of tubes the diameters of which though were much smaller than the width of the birds’ bills. – Feeding of the bee could not be seen in enough detail to know which tubes were exploited.

After this episode the birds were not seen again, their defence was therefore protecting temporarily a food source rather than a territory. Whether the resource had been nectar and/ or pollen, all food of the orange-bellied flowerpecker beside berries and tiny insects (CHEKE et al. 2001), cannot be decided. – The carpenter bees are known to consume nectar and pollen, with the latter being used for provisioning the cells containing their brood.

Discussion

This is the first detailed report on interspecific resource defence cutting across animal phyla in the world, i. e. insects and birds; it raises new questions. That there is competition for food between birds and nectarivorous insects was known for some time. Hummingbirds have been seen fiercely defending their flower resources against large bees and butterflies, with the severity of defense increasing with nectar scarcity (BOYDEN 1978, CARPENTER 1979). Interestingly, the large bees chased the birds in return (see also POHLAND & MULLEN 2008: stingless bees). Competition is also born out by spatial and temporal segregation of the insects and the birds. Similarly Darwin’s finches (*Geospiza fuliginosa*, *G. difficilis*) increase their nectar intake considerably on Galapagos

islands where the large generalist carpenter bee (*Xylocopa darwini*) is absent (SCHLUTER 1986). In general, aggression against insect competitors increases with resource overlap, and is therefore greater within species than between species (review PEIMAN & ROBINSON 2010). – Here I will discuss first causal and then functional aspects of the flowerpecker-bee interaction.

Causal aspects. – Interspecific territoriality among fish (EBERSOLE 1977, MYRBERG & THRESHER 1972, THRESHER 1976, NAKANO & NAGOSHI 1990, LOSEY 1981, LOSEY JR 1982), birds (CURIO 1959, REED 1982, CORDERO & SENAR 1990) and other groups (GREYER 2011) is almost ubiquitous. In spite of vast morphological differences among, e. g., coral fish ranging from a trumpet fish (*Aulostomus maculatus*) or a moray eel (*Gymnothorax moringa*) to small damsels, there are many commonalities shared by all fish allowing them to be classified as fish. Interaction of the fish ‘gestalt’ with their foraging behaviour (diet overlap) and their predatory threat to the offspring then leads to intruder-specific aggression (see Introduction). The underlying cognitive mechanism is, hence, both ‘gestalt-based’ and ‘action-based’. Also in birds aggression displayed toward a heterospecific differs from that elicited by a conspecific contesting the same resource (CURIO 1959, BOYDEN 1978, CORDERO & SENAR 1990). The amazing discriminatory achievement underlying such species- or class-specific aggression could be brought about by either of two different mechanisms. Either there is innate recognition of each heterospecific eliciting a distinct aggressive act restricted to that species, with acts varying qualitatively (birds) or quantitatively (distance from territory, see Introduction). Recognition is achieved by an IRM (Innate Releasing Mechanism) sensu CURIO (1993), i. e. a perceptual mechanism decoding a given stimulus situation in the *absence* of an opportunity for learning about the releasing stimuli involved (CARO 2005: dozens of vertebrates). This operational definition of an IRM leaves room for modifying influences independent from those stimuli to complete or perfect the IRM in question. Applying this concept to interspecific aggression outlined above would demand as many IRMs to exist in the defender as there are discernable releasing stimulus situations as represented by the diversity of intruders. Such a plethora of IRMs (41 in the case of *Eupomacentrus leucostictus*) would probably overtax the perceptual capacity of the defender. And this problem is being exacerbated when intruder and defender belong even to different phyla as is the case here; with arthropods coming into the picture, the number of competitors would soar into the hundreds. Moreover, the similarity between an oscine and a bee ends already after looking at body size, bilateral symmetry and the ability to fly, thus likely overtaxing discriminatory powers of a defender. In a review of the ‘neuroecology’ of competitor recognition including heterospecific aggression GREYER (2011) discusses the underlying perceptual mechanism merely on the basis of straightforward stimulus-response relationships.

Alternatively, experience with the exploitation of a vital resource by the intruder would engender a species-specific cognitive mechanism that could build on a rather stimulus-poor template for any intruder and that becomes tuned to the quality and severity of the exploitation perceived. The underlying RM (Releasing Mechanism) would be 'action-based' rather than 'gestalt-based' in deciphering (innately?) the threat imposed by the intruder. An innate rule of thumb coping with an intruder for the first time could deploy a command like 'Attack every animate object perceived pilfering/touching a resource'. And pilfering/touching then would cause the stimulus of the intruder to become conditioned for the attack quality and intensity elicited by and tailored to a particular intruder in the future. A concept thus combining a 'gestalt-based' object recognition with an 'action-based' recognition would be able to cover the whole range of phenomena from a highly 'gestalt'-specific IRM tuned to an intruder species to a generalized IRM operating in concert with an 'action-decoding' (I)RM. Importantly, this cognitive achievement falls in line with the fact that hummingbirds attack larger butterflies only as soon as they land on the contested flower (BOYDEN 1978). There may be some stimulus-specificity in that hummingbirds chased only the larger insect competitors, thus leaving unscathed the smaller ones like bees, flies and the small skipper butterflies (BOYDEN 1978).

The idea of a cognitive mechanism deciphering detrimental action operating in concert with a general IRM recognizing intruders only broadly predicts three things. a) A novel, allopatric intruder is ignored by the resource-holding keeper. b) As soon as this intruder engages in ecologically detrimental behaviour said keeper would attack. Exactly these conditions hold in an experiment with a bottom-feeding damselfish (*Stegastes fasciolatus*). When being confronted with a novel cichlid intruder the damsel only attacked it when it started to feed in the way as was typical of the damsel, i. e. on the bottom (LOSEY 1981) while it went unscathed when feeding on prey near the surface (LOSEY 1982). This proves that aggression was directed against a detrimental feeding mode rather than to feeding per se. This suggests a third condition to hold: c) Defence relies on action rather than clues betraying the identity of the intruder. This will apply most forcefully where the clues entering an IRM deviate drastically from those of the average competitor as in the present case. Upon the first encounter the 'action-based' mechanism proposed here could then capitalize on the sophisticated powers of species recognition in fish and birds. In fact great tits (*Parus major*) have apparently stored in their memory the appearances of all bird species of the community they are living in (CURIO 1989). This enables them to recognize novel, i. e. allopatric heterospecifics and monitor their actions.

Here I favour the view of a general perceptual mechanism identifying intruders only to the extent that they come to elicit defence via an 'action-based' (I)RM because of the huge disparity between a bee and a bird exploiting the same resource. This idea,

elaborated upon on p. 5 above, falls also in line with the flowerpecker's way of defence: pouncing on the bee while feeding as opposed to merely chasing it in mid air when pilfering was still a mere threat. The precise nature of the defence is context-dependent in a meaningful way (see next section). In hundreds of encounters with either of the two common carpenter bees (*X. latipes*, *X. cuernosensis*) when cruising widely I saw them never chased by a nectarivorous bird.

Only the male defended the flowers whilst his presumed female mate tolerated the presence of the bee, even at very close range. This is best explained by that in birds it is usually the male that takes on himself the lion's share of resource defence.

Adaptive aspects. - MURRAY (1971) had suggested that avian interspecific territoriality results from mistaken identity and, hence, is not adaptive. Given the supreme powers of species-specific identification including most subtle enemy recognition (CURIO 1993) this idea appears little realistic. Furthermore, the resource defence reported above is cutting across phyla, with the adversary not even remotely resembling another bird competitor. Further, even similar, congeneric bird species show species-specific recognition of each other (CORDERO & SENAR 1990). However, heterospecific aggression declines with decreasing phylogenetic relatedness (PEIMAN & ROBINSON 2010).

The adaptedness of the defence by the flowerpecker is further born out by the vigour being geared to the degree of infringement (see above). Second, carpenter bees en route have never been seen chased by birds (see above). Third, in a field experiment, REED (1982) demonstrated that the strength of defence of great tits against chaffinches (*Fringilla coelebs*), when both species were exploiting insects, increases with the pressure from the latter. Finally, various fish tune their aggression finely to the food overlap and risk imposed by heterospecific adversaries (previous section), thus economizing the costs of defence.

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Zusammenfassung

Nahrungsverteidigung eines Blütenpickers gegen eine Holzbiene und ein Wahrnehmungsproblem. - Es wird über eine einseitige Aggression eines Männchens des unter anderem Nektar trinkenden Orangebauch-Blütenpickers (*Dicaeum trigonostigma australe*) gegen die weltweit größte Holzbiene (*Xylocopa latipes*) auf der Insel Panay, Philippinen, berichtet. Der Vogel griff die Holzbiene wiederholt an, während sie an den wenigen Blütenständen eines Baumes (*Nauclea orientalis*, Rubiaceae) wie er und (s)ein Weibchen nahebei Nektar trank. Überdies griff der Blütenpicker die Biene im Flug an und verhinderte so ihr Landen auf den Blüten. Das Weibchen blieb dabei neutral, selbst als es gleichzeitig an demselben Blütenstand trank. Anders als in der genannten Konkurrenzsituation habe ich in insgesamt fünf Jahren Feldarbeit auf den Philippinen Vögel weiträumig fliegende Holzbienen, einschließlich *X. cuernosensis*, nie angreifen sehen. Deshalb wird die beschriebene Aggression des Blütenpickers als Ressourcenverteidigung gedeutet. Der zugrundeliegende Entscheidungsmechanismus wird am besten durch die Annahme eines ‚Aktions-basierten‘ kognitiven Mechanismus zum Erkennen und zur Abwehr ressourcenbedrohender Ereignisse erklärt, weniger gut durch einen eindringlings-spezifischen ‚Art-basierten‘ Erkennungsmechanismus. Vögel und auch Fische verfügen über höchst entwickelte Fähigkeiten zur Identifizierung syntoper Arten, und die Kohlmeise ist sogar fähig, die gesamte Begleitvogel-Fauna ihres Lebensraums ‚im Kopf‘ zu haben. Wegen der großen Anzahl syntoper, als Konkurrenten handelnder Arten nimmt das ‚Aktions-basierte‘ Kognitions-Modell an, dass sie nicht über eindringlings-spezifische, angeborene Auslösemechanismen (AAMs) erkannt und so zum Ziel von Ressourcenverteidigung werden, sondern auf dem Weg über vielleicht angeborenes Erkennen abträglicher konkurrenzbezogener Aktionen. Ferner ist ein angeborenes Erkennen sämtlicher Nahrungskonkurrenten trotz solcher vereinzelt nachgewiesenen Fähigkeiten (‚Art-basiertes‘ Erkennen) durch den vorliegenden Nachweis einer Dekodierungsleistung über Tierstamm-Grenzen hinweg noch unwahrscheinlicher geworden. Auch befähigt eine ‚aktions-basierte‘ Ressourcenverteidigung zu einer sonst nur schwer vorstellbaren Flexibilität, d. h. mit

neuen Konkurrenten fertig zu werden. – Es werden mehrere Argumente für die Anpassungsnatur der beschriebenen Ressourcenverteidigung vorgetragen und damit eine ältere Hypothese der Verwechslung fremder Arten mit Artgenossen verworfen.

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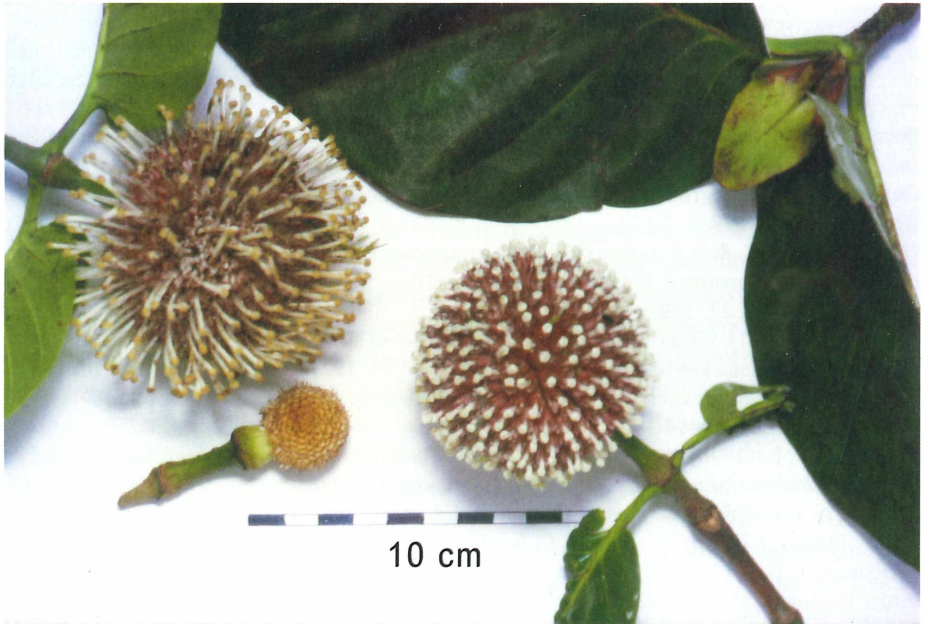


Fig. 1. *Nauclea orientalis* (Rubiaceae) globose flowers. Right: single flowers within the ball are mature and supply nectar. Left: the flowers are withered and their nectar is exhausted. Below left: flower ball totally withered, the single flowers have fallen off. Photo: A. Hamann.

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