

Ground-foraging palm cockatoos (*Probosciger aterrimus*) in lowland New Guinea: fruit flesh as a directed deterrent to seed predation?

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Abstract: Fruit traits that selectively deter vertebrate seed predators without affecting high-quality seed dispersers are said to exhibit directed deterrence. Directed deterrence has been criticized as being unlikely in natural systems, but has rarely been explicitly tested. We evaluated the potential for directed deterrence to explain the double-layered viscous fruit morphology and fruiting phenology of *Terminalia impediens*, a common canopy tree endemic to New Guinea. The large fleshy fruits of this tree are consumed and dispersed by cassowaries (*Casuarius* spp.) and are consumed and killed by palm cockatoos (*Probosciger aterrimus*). Fruit flesh in this tree species appears to function as a deterrent to seed predation by palm cockatoos; the fruits of *T. impediens* fall to the ground before ripening, and are avoided by palm cockatoos until after the flesh has rotted off the hard nut. We found that palm cockatoos are able to prey upon seeds from fruits without flesh on the forest floor more efficiently than they can consume seeds from unripe fruit still on the trees. Further, through foraging preference tests, we found that palm cockatoos largely ignore seeds within ripe fruit on the ground, but readily eat the seeds when the fruit flesh has been removed. Cassowaries consume the fruit whole, when ripe, and defecate seeds in piles away from parent trees, where seed predation rates are lower. These results challenge the prevailing view that fleshy fruits evolved in tight synchrony with high-quality seed dispersers and add support to the non-exclusive hypothesis that aspects of fruit fleshiness may also have evolved as a response to seed predation.

Key Words: cassowary, directed deterrence, dispersal, evolution, fruit–frugivore interaction, morphology, *Terminalia*

INTRODUCTION

The adaptive function of fruit flesh is typically believed to be the facilitation of seed dispersal through the attraction of fruit consumers, many of which will consume the seeds with the fruit pulp, and move viable seeds to locations away from the parent tree (McKey 1975, Snow 1971, van der Pijl 1972). Many fruits, however, have morphological, chemical, and nutritional qualities that deter consumption by vertebrates (Cipollini & Levey 1997a, Herrera 1982). Traits that reduce fruit consumption are thought to occur due to a persistent evolutionary dilemma faced by plants: how to make fruit attractive to seed-dispersing animals and simultaneously unattractive to seed predators (Cipollini & Levey 1997a, Herrera 1982, Howe 1977, Janzen 1977). Directed

deterrence posits that the function of a fruit trait (typically chemical) is to deter low-quality dispersers or seed predators, without deterring high-quality dispersers (Janzen 1979, Schupp 1993, Sorensen 1983). Indirect support for chemically mediated directed deterrence exists in a handful of fruit systems (Cipollini & Levey 1997a, Herrera 1982, Struempf *et al.* 1999; see also Tsahar *et al.* 2002). However, results from experimental tests have been conducted in only two plant genera. In *Solanum* Cipollini & Levey (1997b) found little evidence consistent with directed deterrence, yet in *Capsicum*, Tewksbury & Nabhan (2001) found strong evidence for chemically mediated directed deterrence of seed predators.

The potential for morphological, rather than chemical, fruit traits to selectively deter potential vertebrate seed predators has received limited direct attention (Mack 1998, 2000; but see Willson & Thompson 1982, Willson & Whelan 1990), but may help explain unusual fruit morphologies. In this study, we focus on a complex morphological trait – fruit flesh – and its ability to function

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both as a directed deterrent to seed predators as well as a reward to high-quality seed dispersers.

Terminalia impediens (Combretaceae) is a large canopy tree endemic to lowland and hill forests of New Guinea (Coode 1973, Womersley 1978). It produces large fleshy-fibrous fruit (approximately $60 \times 50 \times 90$ mm) surrounding a single, large stone (Coode 1973, Womersley 1978). Although data from the wild are lacking, fruits develop between March and July in south-eastern New Guinea, and the majority appear to fall to the ground before completely ripening (CEF *pers. obs.*; see also Coode 1973). The unripe fruit consists of hard, undifferentiated pulp surrounding the stone, contrasting with the fleshy, two-layered pulp that surrounds the large, woody stone in ripe fruit. In the ripe fruit, the inner layer of pulp is integrated with the fibrous surface of the stone (see Womersley 1978) while the outer layer forms a sticky, loosely connected mass that may make accessing and cracking the stone more difficult for seed predators. Vertebrate predation on these seeds could thus be influenced by either mechanical (i.e. flesh) or chemical deterrents (Cipollini & Levey 1997a, Herrera 1982, Mack 2000), both of which should change as fruit flesh decays on the forest floor.

A primary vertebrate seed predator across the range of *T. impediens* is the palm cockatoo (*Probosciger aterrimus* Gmelin), a huge seed-eating parrot that appears to be one of the few species capable of cracking the woody stone. At a site in lowland Papua New Guinea, we found preliminary evidence of palm cockatoo seed predation at nearly all *T. impediens* trees visited. Significantly, however, ripe fruits on the ground were largely ignored by ground-foraging cockatoos, who appeared to favour older fruits whose flesh had mostly rotted off, leaving only the relatively dry protective nut as a barrier to seed predation. Additionally, although rodents (*Uromys* spp.) prey upon seeds within old fruits on the ground (CEF *pers. obs.*) fresh fleshy fruits were generally ignored. Thus, fruits of *T. impediens* may be relatively free from vertebrate seed predation from the time they ripen (typically on the ground) to the time that the pulp rots off of the fruits, a period of 10–14 d.

The only consistent seed disperser of *T. impediens* fruits are cassowaries (*Casuaris* spp.; see Mack 1995). These large, flightless birds forage on ripe fruits that have fallen to the ground, ingesting them whole and defecating the seeds in a mass of partially digested pulp some distance away from the parent tree. The large *T. impediens* fruits are generally ignored by canopy foraging frugivores (e.g. flying foxes (*Pteropus* spp.) and hornbills (*Aceros plicatus*)), most likely due to the constraints that gape width places upon the ingestion of large fruit (Wheelwright 1985). In addition, we saw no indication of seed predation of the unripe fruits by the terrestrial fauna (e.g. murids and coleopterans). *Terminalia impediens* thus appears to have a single class of high-quality seed disperser (cassowaries)

whose only incentive to ingest the fruits is the nutritional content of the fruit pulp. In contrast, that same pulp may act as an obstacle to seed predation by palm cockatoos (and other vertebrate seed predators such as *Uromys* spp.), whose nutritional reward comes entirely from breaking the hard stone and consuming the seed.

Significantly, overall fruit morphology in *T. impediens* is distinctive relative to most other *Terminalia* species in the region (except the sympatric *T. kaernbachii*; see Womersley 1978), which generally bear much smaller, canopy-ripening fruits, with less complex flesh (Coode 1973, Womersley 1978). Additionally, other *Terminalia* species studied typically have a greater diversity of seed dispersers and predators (e.g. Snow 1981, Willson *et al.* 1989), suggesting the distinctive qualities of *T. impediens* fruits may represent an evolutionary response to unusual selective pressures.

We set out to test the hypothesis that ripe fruit morphology in *T. impediens* functions as a directed deterrent against seed predation by a specialized seed predator (palm cockatoos). We examine the strength of the relationship between palm cockatoos and *T. impediens*, and the effect of fruit pulp on palm cockatoo foraging behaviours. If the fruit morphology of *T. impediens* functions to deter palm cockatoos while allowing cassowaries sole access to the ripe fruit, when given a choice, palm cockatoos should prefer older, dried fruits (that have had ample time to be ingested by cassowaries) to their fresh, fleshy counterparts. Equally important, the removal and deposition of *T. impediens* seeds away from the parent tree by cassowaries should decrease palm cockatoo predation on those seeds.

METHODS

Movement patterns and ground foraging behaviour of palm cockatoos were investigated at a site along the Nagore River ($6^{\circ} 51' S$, $146^{\circ} 34' E$; 70 m asl) within the Lakekamu–Kunimaipa Basin of southern Papua New Guinea (LKB; for detailed description see Beehler *et al.* 1995). Studies of palm cockatoo movement and foraging behaviour were conducted in 1992 and 1993, throughout the fruiting season of *T. impediens* (April–August).

Cockatoo foraging behaviour

We observed foraging palm cockatoos in the study area to quantify handling times and the prevalence of ground versus canopy foraging. When a cockatoo was encountered foraging on *T. impediens* seeds on the ground or in the canopy, the bird was observed until it gripped a previously unhandled fruit with its bill or

feet. Timing began when the bird first gripped a fruit and continued until the seed was fully extracted (and the endocarp discarded) or until the fruit was dropped (without recovery).

To isolate the effect of the fruit flesh on seed predation, we compared seed predation on ripe, intact 'fleshy' fruits, with predation on 'naked' fruits from which we manually removed all of the fruit flesh, mimicking the condition of the seed after the flesh has rotted and fallen from the fruit. After removing the crop of fallen fruit beneath 10 fruiting *T. impediens* trees (all with canopies ≥ 150 m apart) where one or more groups of palm cockatoos had been previously observed, fleshy and naked fruits were arranged in paired piles beneath each fruiting tree. Paired fruit piles consisted of one pile of five fleshy fruits and one pile of five naked fruits placed on the ground 50 cm apart along a randomly selected compass axis. Previous observations suggest 50 cm spacing provides enough proximity for simultaneous recognition of both piles and enough distance to enable foraging within one pile without disturbing the other. Twelve pairs of piles were randomly placed within a circular band 5–10 m from the base of each of the ten trees. Each pair of piles was at least 4 m from its neighbour. A total of 120 paired fruit piles were arranged in this manner and were checked over a period of 2 wk.

We assessed patterns of seed predation by palm cockatoos away from parent trees by placing an additional 87 paired fruit piles (arranged 5 m apart along five transects) through randomly selected areas in the LKB. All transect points were at least 60 m from the nearest *T. impediens* tree. All paired fruit piles were checked for seed predation by palm cockatoos twice weekly for the duration of each field stay. Seed predation by palm cockatoos within the fruit piles is unmistakable due to the distinctive scars their huge bills leave on the nutshells. Because the fruits in the fleshy piles eventually lose their flesh, functionally negating the experimental contrast, we truncated our experiment after 2 wk.

Cockatoo movement patterns

Daily movement patterns of palm cockatoos were observed from canopy blinds in trees rising above the basin floor (see Beehler *et al.* 1995 for site details). Canopy observations were made during at least three dawn (06h00–09h30), three dusk (16h00–18h30) and two midday (09h30–16h00) periods per week for the 7 wk between 18 June and 5 August 1993. Fifty-eight observation bouts were conducted with an average duration of 3 ± 1.06 h per bout (range: 1.5–5.0 h). All (eight) *T. impediens* trees visible from the two canopy blinds were mapped. For each cockatoo observation, we noted whether the bird(s) were moving above or within

the canopy and noted whether or not birds took flight or alighted in proximity to known fruiting trees.

Statistical analyses

Handling times were compared using Student's t-tests. The significance of contrasts between midday and dusk/dawn cockatoo flight patterns was tested using a Chi-square test. We tested the hypothesis that cockatoo movement patterns were significantly associated with fruiting *T. impediens* trees using a chi-square goodness-of-fit test with the null hypothesis that observations of cockatoo flights to and from *T. impediens* versus other tree species did not deviate from an even 1:1 ratio. We chose this ratio because approximately one half of the area visible from the blinds was categorized as proximal to the eight mapped *T. impediens* trees, and random cockatoo movements, by chance, would have been associated with the trees 50% of the time. We investigated cockatoo seed predation on fleshy and naked fruit piles using a proportional hazard survival analysis called Cox Regression (Cox 1972, Kalbfleisch & Prentice 1980). Cox regression allowed us to analyse seed predation rates while accounting for seed piles which were not depredated during the experiment (censored data). We included tree identity and fruit condition (fleshy vs. naked) as categorical covariates in a global model, and removed variables that were not significant ($P > 0.1$) to produce a reduced model. As piles of fruit were generally eaten in their entirety, we treated each pile as predated or whole at the end of each sampling period, and examined the effect of fruit condition on the chance that a pile would be depredated.

RESULTS

Cockatoo foraging behaviour

We obtained 47 observations of palm cockatoos foraging during 291 h of combined observation effort in canopy blinds (~ 167 h) and walking trails (~ 125 h). Consistent with incidental evidence of cockatoo seed predation at nearly all fruiting *T. impediens* trees (58 of 60), 35 (75%) of the foraging observations we obtained were instances of seed predation on *T. impediens* seeds. In 13 cases (37%) birds were foraging on the ground, while in the remaining 22 cases (63%) birds were foraging in the canopy. Importantly, the rate of ground-foraging is likely conservative: relative to canopy-foraging individuals, birds foraging on the ground are much more likely to flush before being detected (CEF *pers. obs.*). All ground-foraging events resulted in successful predation of the seed with median handling times for seed extraction under

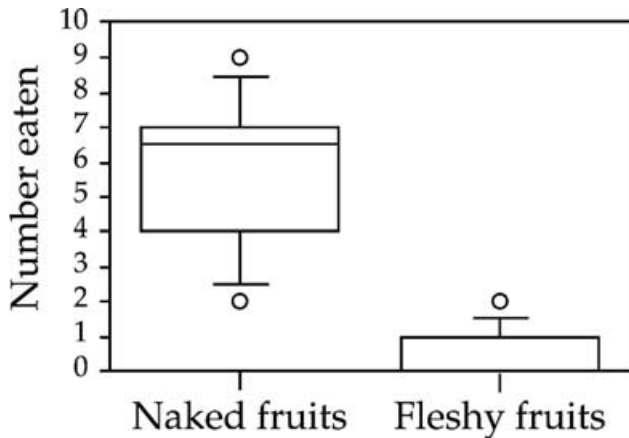


Figure 1. Box plots comparing mean numbers of fleshy and naked fruits eaten by palm cockatoos in paired fruit piles placed under ten fruiting *Terminalia impediens* trees (monitored for 2 wk; see text) in the Lakekamu–Kunimaipa Basin of Papua New Guinea.

2 min (median = 2.2 min, range = 2.2 min, $n = 13$). In contrast, 27% (6 of 22) of the canopy foraging events were unsuccessful, with palm cockatoos dropping the stone during processing, and median handling time for successful consumption of seeds was 6 min (range = 13.4 min, $n = 16$). Cockatoos were thus more successful ($\chi^2 = 4.3$, $P = 0.039$) and expended less effort ($t = 4.02$, $df = 27$, $P < 0.001$) when foraging on the ground.

Palm cockatoo seed predation was detected in at least two (and up to 11) of the 12 paired fruit piles beneath each of the 10 focal trees. Tree number was not significant in our global model (Wald = 13.0, $P < 0.16$), and removal did not change the remaining variable (seed condition; fleshy vs. naked), thus our reduced model included only seed condition. Seed predation under *T. impediens* was more than 15 times higher on piles of naked seeds than on piles of fleshy seeds (Wald = 31.5, $P < 0.0005$, $\text{Exp}(B) = 0.234$, 95% CI: 0.141–0.389), with greater than 40% of all naked seed piles preyed on by cockatoos in 2 wk and less than 3.5% of fleshy fruited piles removed over the same period (Figure 1). In piles placed away from parent trees, no predation of any kind was observed over the 2-wk period.

Cockatoo movement patterns

During midday, palm cockatoo flights were nearly all below the level of the tallest canopy trees (96 of 99 flights), whereas flights during dusk/dawn time periods were primarily (36 of 42 flights or 86%) above the canopy ($\chi^2 = 101$, $P < 0.001$). Because we could not reliably assess whether a cockatoo below the canopy alighted or took flight in proximity to one of the fruiting trees, we only used flights during the dusk/dawn period to compare patterns of cockatoo movement with the distribution of

fruiting *T. impediens*. We were able to clearly see a bird alighting or taking flight in 33 of the 42 dusk/dawn observations. During these 33 observations, cockatoos showed a significant association with fruiting *T. impediens* ($\chi^2 = 13.4$, $P < 0.001$).

DISCUSSION

The simultaneous influence of seed predators and seed dispersers on the evolution of fruit traits has been recognized since at least the 1970s (Janzen 1971, 1983; Howe & Estabrook 1977). Whether the fruit trait in question is chemical, morphological, or nutritional, a trait that effectively filters potential fruit consumers, allowing only quality seed dispersers access to the fruit, is highly advantageous. The evolution of this directed deterrence, however, requires both predictable and evolutionarily stable differences in the quality of different vertebrate consumers, and a trait that consistently deters only the group of lower-quality dispersers or seed predators. In the current study system, morphological properties of *T. impediens* fruit appear to fit this definition, as they selectively deter a specialized seed predator without hindering the primary disperser.

Observations of palm cockatoo movement and foraging patterns in the LKB suggest that, at least for the periods we observed, cockatoos are specializing on the heavily protected seeds of *T. impediens*. First, dusk and dawn movements of palm cockatoos showed a significant association with fruiting *T. impediens* trees. Second, frequencies of palm cockatoo predation on *T. impediens* seeds (both in our incidental observations and in the paired fruit piles under fruiting trees) suggest that rates of cockatoo seed predation in this system are high relative to those reported for other vertebrate seed predators (Janzen 1971, Lanner 1988, Tomback 1982). Results of this study cannot determine whether or not cockatoo movements and foraging intensity have had an evolutionary effect on *T. impediens* fruit morphology, but taken together, our observations of cockatoo movement and foraging patterns indicate a strong association between palm cockatoos and the heavily protected seeds of this tree.

The dramatic difference in predation rates seen between fleshy and naked seeds below parent trees suggests that the flesh surrounding *T. impediens* seeds functions as efficient protection against a primary seed predator, palm cockatoos (Figure 1). This protection appears to extend the time viable seeds can persist unmolested on the forest floor, where they can be ingested and dispersed by cassowaries. Interestingly, dispersal by cassowaries results in the exposure of naked seeds, as cassowaries consume much of the flesh. However, by dispersing the seeds away from the high seed density under the parent trees where palm cockatoos

forage, cassowaries may be allowing the seeds to escape predation – in our data, seeds away from parent trees escaped predation entirely. All of these results are consistent with the flesh of *T. impediens* seeds simultaneously deterring predation by a specialized seed predator, and attracting high-quality dispersers that disperse seeds to safe-sites away from parent trees. Additionally, *T. impediens* fruits fall directly to the ground, creating a strongly clumped distribution of fruit and seed resource for both predators and dispersers. This, coupled with the existence of a single group of dispersers and an apparently specialized vertebrate seed predator, creates ideal conditions for the evolution of directed deterrence.

Importantly, if significant numbers of naked fruits exist on the ground, unripe *T. impediens* fruits in the canopy may be less attractive to palm cockatoos (due to handling times). Additionally, unripe fruits should be generally unattractive to canopy foraging frugivores such as flying foxes which likely represent low-quality dispersal opportunities for the tree relative to cassowaries. For cockatoos, handling times of naked fruits on the ground are significantly shorter and success rates significantly higher than for unripe fruits in the canopy, suggesting ground-foraging may be energetically less costly so long as old seeds are available. In contrast, canopy-foraging frugivores may be deterred by chemical, as well as morphological, protection of unripe fruit; theory predicts a high degree of chemical defence in unripe fruits (Herrera 1982). Because palm cockatoos do not ingest or masticate the flesh of *T. impediens* and do access seeds from unripe fruit (presumably chemically protected against frugivory), chemical defence against cockatoos is unlikely. Therefore, unlike other systems in which directed deterrence has been tested or postulated (Tewksbury & Nabhan 2001), the deterrent trait in this case (ripe flesh) must function selectively within a single vertebrate order, separating an avian disperser from an avian predator. Such selectivity within consumer groups would be difficult to achieve chemically (Cipollini & Levey 1997a), further suggesting that certain physical pulp traits are driving the avoidance by palm cockatoos of ripe *T. impediens* fruits on the ground.

Ultimately, the evolution of the two-layered, fleshy-fibrous pulp of *T. impediens* as a directed deterrent to cockatoo predation, and attractant to cassowaries, is contingent upon a history of stable interaction among these taxa. Fossil and molecular evidence suggest that both the genus *Probosciger* and the genus *Casuarinus* date from at least as far back as the early Miocene (Brown & Toft 1999, Schodde & Calaby 1972, Sibley & Alquist 1990). Because New Guinea was submerged at this time, colonization by plants and animals did not occur until the mid- to late-Tertiary (Schodde & Calaby 1972). The ancestor of *T. impediens* (now endemic) thus likely evolved in association with ancestors of both cassowaries and

palm cockatoos, both of which appear to exert strong selective forces on *T. impediens*, providing the evolutionary context for these species to influence fruit morphology.

The incidence of fruit flesh functioning as a deterrent to seed predation may be more common than has been appreciated to date. Even within relatively poorly known New Guinean systems, at least two other fruits appear to show defensive adaptations to cockatoo predation (*Terminalia kaernbachii* (CEF pers. obs.) and *Cerbera floribunda* (Mack & Wright 1996)). Additionally, spicules within the succulent pulp of *Gnetum* spp. deter rodent seed predators until the pulp has been removed (Mack 2000). Beyond New Guinea, Silvius & Fragoso (2002) provide strong experimental evidence for morphologically mediated directed deterrence by showing that both the exocarp and mesocarp of some palm fruits protect seeds from beetle infestation.

CONCLUSIONS

Directed deterrence has been postulated as one adaptive function of secondary metabolites in ripe fruit. We suggest that morphological and nutritional qualities of fruit can also be used to separate high- and low-quality vertebrate seed dispersers, and that these fruit traits may often function both as deterrents and attractants to fruit consumers. The foraging patterns of palm cockatoos documented here (including the first published records of consistent ground-foraging) suggest these birds are specializing on the seeds of *T. impediens* and indicate a significant avoidance of the flesh of fruits that are at the peak of their attractiveness to cassowaries. Whereas most studies concerning fleshy fruit evolution have focused on the role of fruit traits in promoting seed dispersal (Herrera 1987, Howe 1977, 1979, 1980; Howe & Estabrook 1977, Jordano 1995, McKey 1975, Snow 1971), Mack (2000) used evidence from the fossil record, modern fruit morphology, and dispersal syndromes to argue that fleshy fruits may have initially evolved as a defence against seed predation. Indeed, the sheer diversity of morphological, chemical and nutritional characteristics of different fruits, many of which share the same dispersers, suggests that fruit may have multiple adaptive functions (Cipollini & Levey 1997a, Schmitt *et al.* 1995, but see Jordano *et al.* 2003). The unusual fruit characteristics of *T. impediens* appear strongly influenced by the dual selective pressures of a dominant seed predator and a dominant seed disperser. Comparative investigations of fruit morphology, phenology, nutrition and chemistry on this and related species would greatly assist in isolating phylogenetic effects on fruit morphology from local adaptations directed at deterring seed predators and attracting cassowaries. This system may be particularly amenable to such analysis, due to the limited number of seed dispersers

and seed predators, and the potential for consistent selective pressures over the entire range of the species.

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