Short Communications

Fruit selection in the olive thrush: the importance of colour

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Free-living olive thrushes *Turdus olivaceus* were offered a choice of wild olive *Olea africana* fruit of four colours, representing four ripeness categories. The thrushes ate mostly black fruit (ripest), followed by maroon (ripe) and olive-coloured (partially ripe) fruit. When riper fruit was unavailable, the thrushes selected more maroon or olive-coloured fruit. Green fruit (unripe) were never eaten, even when these were the only ones available. When offered pieces of dyed pear *Pyrus communis*, the thrushes preferentially selected orange pieces, followed by red and black pieces. Green pieces were never eaten. The results indicated that olive thrushes selected fruit on the basis of fruit colour, and that colour preferences differed between the two types of fruit offered.

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Fruit-eating birds preferentially eat particular fruit types rather than others (Moermond & Denslow 1985). Many factors influence fruit choice in frugivorous birds, including accessibility, availability and abundance of fruit (Davison 1962; Kantak 1979; Sorensen 1983; Moermond & Denslow 1985; Sallabanks 1993), fruit presentation (Kantak 1979; Moermond & Denslow 1985; Wheelwright & Janson 1985; Levey 1987b; Wheelwright 1988; Willson, Graff & Whelan 1990; Sallabanks 1993), fruit size (Wheelwright 1988; Levey 1987a), sugar content or taste (Davison 1962; Sorensen 1983; Moermond & Denslow 1985; Levey 1987b), pulp texture (Moermond & Denslow 1985; Wheelwright & Janson 1985; Wheelwright 1988; Sallabanks 1993), ultra violet (UV) reflectance of berries (Burkhardt 1982), total seed mass and seed-to-pulp ratios (Wheelwright & Janson 1985; Herrera 1987), and possibly insect larvae exit holes (Sallabanks 1993).

Fruit colour may influence fruit selection in birds (Snow 1971). Colour is a key characteristic of fruit, affecting whether or not the fruit is noticed and/or consumed (Wheelwright & Janson 1985). Birds have well developed colour vision, particularly in the orange-red part of the spectrum (Burkhardt 1982). Hence, fruit that is red, orange, black or purple when ripe is usually bird-dispersed (Moermond & Denslow 1985; Moermond, Denslow, Levey & Santana 1987; Willson *et al.* 1990).

Many explanations have been suggested for the significance of colour in bird-dispersed fruits. Changes from an inconspicuous, cryptic colour (e.g. green) to a conspicuous colour (e.g. orange) when ripe (Snow 1971; Stiles 1982) may signal ripeness to birds (Snow 1971). Colour may increase visibility by providing contrast between the fruit and the background (Stiles 1982; Knight & Siegfried 1983).

Colour changes in fruit are potentially beneficial to both the plant and frugivorous birds, and in this sense, probably arose as a co-evolutionary phenomenon. Birds benefit through being able to discern differences in nutritional value associated with ripening (Foster 1977), which reduces the costs of lost foraging opportunities. Plants may benefit from reduced feeding attempts on unripe fruit, thereby being protected against potential damage to the developing embryo enclosed within the seed (Knight & Siegfried 1983).

The aim of the study was to ascertain whether or not colour influenced fruit selection in free-living olive thrushes *Turdus olivaceus*. Specifically, we sought to answer three questions: (1) Do thrushes preferentially select ripe wild olive fruit? (2) Are less ripe fruit accepted when fully ripe fruit are not available? (3) Are the choices made by the birds influenced specifically by the colours of the fruit?

The present study was carried out at two sites: the Johannesburg Zoological Gardens, Gauteng (26°12'S; 28°14'E), and a suburban garden in Boksburg, approximately 40 km east of the zoo.

Preliminary observations of their feeding behaviour at the zoo revealed that thrushes fed mostly on fruit of the wild olive *Olea africana* that had fallen from the trees. Closer observation revealed that both ripe and unripe fruit were present on the ground beneath the trees. Hence, foraging thrushes were confronted by a choice of fruit of varying ripeness.

Tests were conducted at the zoo on 12 consecutive days. At the start of tests, wild olives were collected from trees on the zoo grounds and classified according to four ripeness categories based on colour: unripe (green), partially ripe (olive-coloured), ripe (maroon) and fully ripe (black). At 12h00 each day, 20 wild olives of each of the ripeness categories were placed randomly in a cleared 50 × 50-cm patch situated under a wild olive tree. At 14h00, remaining fruit were collected and the number of fruit of each colour eaten by the thrushes was recorded. During tests, the patch was constantly monitored from a distance of 4 m to ensure that only thrushes were consuming the fruit offered. Four to six thrushes visited the patch during each test period.

Three kinds of experiments were undertaken at the suburban garden, comprising choice, exclusion and substitution studies. The choice experiment took place for 10 days, in two sessions per day: morning (07h00–11h00) and afternoon (13h00–17h00). At the start of each session, 10 wild olives of each ripeness category collected at the zoo were placed in a 15 cm diameter dish. The dish was placed on a table in the garden at the start of each session. At the end of each session, remaining fruit were collected and the number of fruit of each ripeness category eaten was recorded. The experimental setup was monitored during each session from a distance of 4 m to ensure that only thrushes were consuming the fruit in the dish. Fewer fruit were offered to the birds at the garden than at the zoo as only one pair of thrushes visited the garden.

The exclusion experiment comprised a series of colour elimination tests, during which fruit of selected colours were excluded from the test. This study was conducted over a 30 day period. At 13h00 each day, a selection of wild olives was placed in a 15cm diameter dish. Remaining fruit were collected at 17h00 each day and the number of fruit of each col-

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our taken by the thrushes was recorded. During the first 10 days, 10 each of maroon, olive-coloured, and green fruit were placed in the dish, while black fruit were excluded. For the next 10 days, maroon and black fruit were omitted and the birds were offered only 10 olive-coloured and 10 green fruit. Ten green wild olives only were used during each of the last 10 days of the exclusion test.

In the substitution experiment, which was conducted for 10 consecutive days, dyed pieces of pear *Pyrus communis* were offered instead of the wild olives. Pears were skinned and cut into small squares that were similar in size to the wild olives. These pieces were dyed with Robertsons™ food dye. Owing to the difficulty of obtaining specific required colours while mixing the various coloured dyes, the fruit pieces could not be dyed so as to look like the wild olives. Thus, the fruit pieces were dyed green, orange, red and black, representing fruit colours found in nature.

Because all other characteristics of the pear pieces (i.e. shape, size, texture, smell and taste) were held constant and only colour was varied, this experiment aimed to establish whether colour alone influenced fruit selection by olive thrushes. Ten each of green, orange, red and black dyed pieces of pear were placed in a 15 cm diameter dish at 13h00 each day. Remaining pieces were collected at 15h00, and the number of pieces of each colour eaten was recorded. Missing pieces were presumed to have been eaten by the thrushes since no other bird species was observed to feed in the dish. The pear pieces were left in the dish for only 2 h per day to avoid desiccation, which potentially could have influenced the feeding behaviour of the thrushes.

Statistical analysis was performed using the Kruskal-Wallis test (two-tailed; Zar 1984) with follow-up multiple range tests. Because we could not distinguish individual thrushes, the days of the experiment formed the replicates when comparing the different coloured fruit taken during each experiment.

Choice tests conducted at the zoo showed that black wild olives were taken significantly more than maroon ones, which, in turn, were taken significantly more than olive-coloured fruit (Table 1; $H = 24.64$, $p < 0.0001$). Green fruit were never eaten, so data in respect of this fruit type were omitted from the statistical analysis.

Similar to the situation at the zoo, thrushes in the suburban garden ate significantly more black than maroon fruit, which were chosen significantly more than olive-coloured fruit (morning sessions: $H = 22.28$, $p < 0.0001$; afternoon sessions: $H = 20.87$, $p < 0.0001$). Green fruit were never taken (Table 1). When black fruit were excluded, the thrushes took significantly more maroon fruit than they did when black fruit was available ($H = 14.46$, $p < 0.001$; Table 1). When only green and olive-coloured fruit were offered, significantly more of the latter fruit were eaten than was the case when all four fruit colours were present ($H = 25.75$, $p < 0.0001$). The thrushes investigated but never ate any green fruit when all other coloured fruit were excluded from tests (Table 1). Absence of beak marks on the fruit suggested that they did not sample (i.e. taste) the green fruit.

In substitution tests, the thrushes took significantly more orange-coloured pear pieces (mean ± 1SE: 9.2 ± 0.34) than they did red ones (2.6 ± 0.86; $H = 22.56$; $p < 0.0001$). Only a few pieces of black fruit (0.2 ± 0.13) were eaten, and green pieces were ignored. The thrushes showed a hierarchical feeding strategy. They first ate all orange pieces present, and only then ate red pieces. Black pieces were eaten only once all red pieces had been consumed.

Table 1 Number (mean ± 1SE) of each colour of wild olive fruit taken by the thrushes at the Johannesburg zoo and the suburban garden during the experiment types indicated. Green fruit were not eaten and the data for this fruit type are thus excluded from the table. Ranges are given in brackets. nf = fruit colour not offered

Study site/ Experiment type	Wild olive fruit colour		
	Olive	Maroon	Black
Johannesburg zoo			
Choice tests	0.92 ± 0.83	4.75 ± 1.47	14.8 ± 1.10
	(0–10)	(0–16)	(8–20)
Suburban garden			
Choice tests			
morning session	0.20 ± 0.13	1.90 ± 0.33	6.60 ± 0.45
	(0–1)	(0–3)	(4–9)
afternoon session	0.20 ± 0.13	1.00 ± 0.62	6.50 ± 0.75
	(0–1)	(0–6)	(3–10)
total	0.20 ± 0.09	1.45 ± 0.36	6.55 ± 1.10
	(0–1)	(0–6)	(3–10)
Exclusion tests			
excluding black	2.40 ± 0.09	8.30 ± 0.37	nf
	(5–9)	(7–10)	
excluding black and maroon	6.90 ± 0.43	nf	nf
	(5–9)		

It appears that the thrushes selected wild olive fruit on the basis of colour, and hence ripeness. Further, the test using dyed pear pieces confirmed that the thrushes made choices based on colour alone.

At both of the study sites, the thrushes preferentially selected black (the ripest) wild olives. The second most selected fruit colour was maroon, which represented fruit that were more or less ripe. Exclusion tests indicated that the thrushes consumed more maroon and olive-coloured fruit when black fruit were not available. In all tests, green fruit were never eaten. It appears therefore that thrushes do eat less ripe fruit, but preferentially choose the ripest fruit available. Completely unripe fruit was always avoided.

While black wild olives were most frequently taken during choice experiments, orange-coloured pear pieces were favoured over other coloured pieces during substitution tests. Wheelwright & Janson (1985) suggest that the response to colour by birds depends on particular circumstances. For example, a red raspberry is nutritious, a red blackberry is unpalatable, and a red beetle is probably poisonous. This implies that although red is a common colour of fruits preferred by birds (Ridley 1930), there is nothing inherent in the colour red that signals edibility or ripeness. Thrushes at the zoo consume large quantities of orange *Pyracantha angustifolia* berries (pers. obs.) which are relatively flat, and the square pieces of pear that were offered used in substitution

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tests may have resembled these berries in shape more closely than they did the wild olives. Thus, it is possible that the thrushes perceived the pear pieces as more similar to *P. angastifolia* fruit, and for this reason, ate the orange pear pieces first; *P. angastifolia* berries are black when rotten, and would therefore probably be unpalatable.

Davison (1962) offered frugivorous birds several species of fruit of different colours, and observed that they ate similar quantities of different coloured fruits of different species. Davison concluded that colour was of little significance in fruit choice in birds. However, Davison did not consider that colour preferences by birds could vary according to the species of fruit offered, as has been demonstrated by McPherson (1988) and the present study. Similarly, Willson *et al.* (1990) found that colour was important in fruit selection in frugivorous birds, and that colour preferences varied according to the circumstances under which fruit were offered.

Two conclusions can be reached in the present study: (i) colour is important in fruit selection in olive thrushes; and (ii) colour preferences vary depending on the type of fruit offered.

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References

BURKHARDT, D. 1982. Birds, berries and UV. *Natuurwissenschaften* 69: 153–157.

DAVISON, V.E. 1962. Taste, not colour, draws birds to berries and seeds. *Audubon* 64: 346–350.

FOSTER, M.S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* 58: 73–85.

HERRERA, C.M. 1987. Vertebrate-dispersed plants of the Iberian peninsula: a study of fruit characteristics. *Ecol. Monog.* 57: 305–331.

KANTAK, G.E. 1979. Observations on some fruit-eating birds in Mexico. *Auk* 96: 183–186.

KNIGHT, R.S. & SIEGFRIED, W.R. 1983. Inter-relationships between type, size and colour of fruits and dispersal in southern African trees. *Oecologia* 56: 405–412.

LEVEY, D.J. 1987a. Seed size and fruit handling techniques of avian frugivores. *Am. Nat.* 129: 471–485.

LEVEY, D.J. 1987b. Sugar-tasting ability and fruit selection in tropical fruit-eating birds. *Auk* 104: 173–179.

McPHERSON, J.M. 1988. Preferences of cedar waxwings in the laboratory for fruit species, colour and size: a comparison with field observations. *Anim. Behav.* 36: 961–969.

MOERMOND, T.C. & DENSLOW, J.S. 1985. Neotropical avian frugivores: patterns of behaviour, morphology, and nutrition, with consequences for fruit selection. *Am. Ornithol. Union Monogr.* 36: 865–897.

MOERMOND, T.C., DENSLOW, J.S., LEVEY, D.J. & SANTANA, E.C. 1987. The influence of context on choice behaviour: fruit selection by tropical birds. In: Quantitative analysis of Behaviour VI: foraging. (Eds) M. Commons, S. Shettleworth & A. Kacelnik. Lawrence Earlbaum Publ. pp. 229–254.

RIDLEY, H.N. 1930. The dispersal of plants throughout the world. L. Reeve. Kent, England. 176pp.

SALLABANKS, R. 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology* 74: 1326–1336.

SORENSEN, A.E. 1983. Taste aversion and frugivore preference. *Oecologia* 36: 117–120.

SNOW, D.W. 1971. Evolutionary aspects of fruit-eating by birds. Ibis 113: 194–202.

STILES, E.W. 1982. Fruit-flags: two hypotheses. *Am. Nat.* 120: 500–509.

WHEELWRIGHT, N.T. 1988. Fruit-eating birds and bird-dispersed plants in the tropics and temperate zone. *Trends Evol. Ecol.* 3: 270–274.

WHEELWRIGHT, N.T. & JANSON, C.H. 1985. Colours of fruit displays of bird-dispersed plants in two tropical forests. *Am. Nat.* 126: 777–799.

WILLSON, M.F., GRAFF, D.A. & WHELAN, C.J. 1990. Colour preferences of frugivorous birds in relation to the colours of fleshy fruits. *Condor* 92: 545–555.

ZAR, J.H. 1984. Biostatistical analysis, 2nd Edition. Prentice-Hall Inc., New York.

Stomach contents of 19 species of small mammals from Swaziland

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The stomach contents of 14 species of Rodentia and five species of Insectivora are reported from Swaziland. The importance of different food types in the diet of these species was estimated using two methods. The results of the frequency of occurrence method closely mirror those of the proportional contribution method. The rodents exhibited a wide range of diets. *Otomys* species were strictly herbivorous, while only three species (*Mus minutoides*, *Tatera leucogaster* and *Dendromus mystacalis*) were observed to have high proportions of all food types in their stomachs. All other rodents fed on green plant matter and seeds, in varying proportions. Shrews were predominantly insectivorous.

The diets of most southern African small mammals have been recorded as anecdotal observations (e.g. Rautenbach 1982; Skinner & Smithers 1990). More detailed studies have been conducted in the Karoo (Kerley 1989, 1992), KwaZulu-Natal Drakensberg (Rowe-Rowe 1986) and KwaZulu-Natal midlands forest (Wirminghaus & Perrin 1992). However, no detailed studies have been undertaken on small mammal diets in the extensive moist savannas of southern Africa. Furthermore, no previously published research has been conducted on any aspect of small mammal communities of Swaziland.

This study was conducted at eight localities (Table 1) in all four geographical regions of Swaziland. Sites varied greatly in climate, geology, altitude and plant community composition (Table 1). Rainfall is highest, and daily maximum and minimum temperatures are lowest, at the highveld sites. In contrast, the lowveld sites experience higher temperatures and a lower annual rainfall. The vegetation of the middleveld,

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