Feeding behaviour of avian dispersers of mistletoe fruit in the Loskop Dam Nature Reserve, South Africa

S.K.B. Godschalk
Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch

The dispersal of three mistletoe species [*Tapinanthus* (formerly *Loranthus*) *leendertziae*, *T. natalitius* ssp. *zeyheri* and *Viscum combreticola*] by birds was studied in the Loskop Dam Nature Reserve, South Africa. Eight of the 27 species of frugivorous birds present were observed feeding on mistletoe fruit. The yellowfronted tinker barbet *Pogoniulus chrysoconus* was the most important single disperser of mistletoes, consuming 64%, 80% and 94% of the fruit of the above mistletoe species respectively, and being behaviourally most suited to the dispersal of mistletoe seed. The other seven avian species were incidental mistletoe fruit eaters. Seasonal variations in mistletoe eating by different birds are mainly related to the preference for *Tapinanthus* fruit by species other than the tinker barbet. Three ways of handling mistletoe seeds are described: regurgitation (in more than 80% of the cases), defaecation and 'pecking'. Very few interactions between birds occurred on mistletoe plants. No interspecific aggression was observed but intraspecific aggression was evident in the tinker barbet. Less than 50% of *Tapinanthus* and less than 20% of *V. combreticola* seeds were carried away from the parent plant or its host. Few seeds were carried away more than 50 m from the parent plant. Regurgitation is most important for mistletoe dispersal generally, but defaecation may be more important for long-distance dispersal and dispersal of the smaller-seeded *Viscum* species.
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Die verspreiding van drie voëlentsoorte [*Tapinanthus* (voorheen *Loranthus*) *leendertziae*, *T. natalitius* ssp. *zeyheri* en *Viscum combreticola*] deur voëls is bestudeer in die Loskopdam-natuurreservaat, Suid-Afrika. Daar is waargeneem dat agt van die 27 vrugtevretende voëlsoorte teenwoordig, voëlentvrugte vreet. Die geelkoptinker *Pogoniulus chrysoconus* was die belangrikste enkele verspreider van voëlente. Dit het onderskeidelik 64%, 80% en 94% van die vrugte van die bogenoemde voëlentsoorte verorber en was met betrekking tot gedrag die mees geskikte vir die verspreiding van voëlentsade. Seisoenale wisselinge in die vreet van voëlentvrugte deur verskillende voëls hou hoofsaaklik verband met die voorkeur vir *Tapinanthus*-vrugte deur die voëlsoorte anders as die tinker. Drie maniere van hantering van voëlentsade word beskryf: opbring (in meer as 80% van die gevalle), ontlasting en 'pik'. Baie min wisselwerking tussen voëls het op voëlentplante voorgekom. Geen tussensoortige aggressie is waargeneem nie maar binnesoortige aggressie was duidelik by die tinker. Minder as 50% van *Tapinanthus*- en minder as 20% van *V. combreticola*-sade is van die ouerplant of sy gasheer weggedra. Opbring is die belangrikste metode vir verspreiding van voëlent in die algemeen, maar ontlasting is moontlik belangriker vir langafstandverspreiding en verspreiding van die *Viscum*-soorte met kleiner sade.
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S.K.B. Godschalk
Present address: South African Defence Force, Logistics Division, Private Bag X319, Pretoria, 0001 Republic of South Africa

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Frugivorous birds play important roles in the dispersal of plant seeds. The feeding behaviour of such frugivores influences the dispersal strategies of the plants concerned, and, on the other hand, the plants' characteristics may influence the feeding behaviour of its dispersers. A whole spectrum of fruit-dispersal strategies exists. The theoretical aspects of these systems have received much attention during the last decade (Snow 1971; Morton 1973; McKey 1975; Howe & Estabrook 1977; Howe 1979; Snow 1981). However, very little research on the dispersal of plants by frugivorous birds has been undertaken in Africa.

Bews (1917) pointed to the lack of detailed information on the feeding habits of South African birds, particularly in relation to the dispersal of plant seeds. Phillips (1924, 1926a, 1926b, 1927, 1928, 1931), working in the Knysna forests, was the first scientist to investigate and report on the role of fruit-eating birds in the dispersal of plants in South Africa. Only recently (Frost 1980; Glyphis, Milton & Siegfried 1981; Knight & Siegfried 1983) has this subject regained attention.

The fruit-frugivore interaction is most important in mistletoes because the parasitic growing habit poses special problems with respect to seed dispersal (Kuijt 1969). Apart from scattered notes (see Godschalk 1979 for references before 1979; Dowsett-Lemaire 1982) and a recent study by Frost (1980), very little is known about the dispersal of mistletoes by birds in Africa. Even less has been published on the behaviour of mistletoe-eating birds in relation to the dispersal of South African mistletoes. The only substantiated reports are those by Cowles (1959), Frost (1980) and Dowsett-Lemaire (1982). This is the first study reporting in detail on the dispersal of South African mistletoes. It deals with the different avian frugivores involved in the dispersal process as well as those aspects of the birds' feeding and post-feeding behaviour related to the dispersal of mistletoe seeds in Africa.

Study area and Methods

The study was carried out in the Loskop Dam Nature Reserve (25°26′S/19°19′E), Transvaal, South Africa, from March 1977 to April 1978 (April 1977 excluded). The reserve is situated in Mixed Bushveld (Acocks 1975), an extremely heterogeneous veld type. The most common trees are *Acacia caffra* and *Combretum apiculatum*. The vegetation of the reserve has been described in detail by Theron (1973) and the avifauna by Baker (1970), supplemented by Godschalk (1981). According to Theron (1973) six species of mistletoe occur in the reserve. This study concentrated on the three common species *Tapinanthus* (formerly *Loranthus*) *leendertziae, T. natalitius* ssp. *zeyheri* and *Viscum combreticola*, with incidental records on *Erianthemum* (formerly *Loranthus*) *ngamicum* and *V. rotundifolium*.

Observations were made at fruit-bearing plants of the three common mistletoe species with the aid of 7 × 50 binoculars, spoken into a tape recorder and afterwards played back. The statistical data in this paper are based on 929 h (198, 193 and 538 h, respectively) of observation on the three common mistletoe species.

All frugivorous birds observed within 40 m of mistletoe plants under observation were recorded (the scientific names of these bird species appear in Appendix 1). When frugivorous birds visited fruit-bearing mistletoe plants, notes were taken of the following aspects

— species and number of bird(s) visiting
— time of day when visiting took place
— feeding technique used
— colour of fruit eaten
— duration of various components of feeding process
— number of fruits eaten per feed
— number of fruits eaten per visit
— duration of visit
— interactions between birds at mistletoe plants
— the distance of post-feeding flights
— location of seed deposits.

Each mistletoe fruit eaten was taken as a feeding record. All observations of yellowfronted tinker barbets feeding on items other than mistletoe fruit were recorded. Several species of frugivores were kept in captivity to collect additional data on some of the above-mentioned aspects.

The number of trees and of other fruit-bearing mistletoes were counted within a radius of 20 m (area approximately 0,125 ha) of fruit-bearing mistletoe plants under observation.

Results and Discussion

Mistletoe-eating bird species

Twenty-seven avian frugivore species were recorded within 40 m of mistletoe plants (Appendix 1) but only eight of these species were observed actually to eat mistletoe fruit (Table 1).

The yellowfronted tinker barbet is by far the most important avian consumer of mistletoe fruit in the study area, taking between 64% and 94% of the three common mistletoe species, thereby overshadowing the importance of all other avian frugivores. It was the only avian species observed to eat fruit of all five mistletoe species in the study area throughout their fruiting periods and the only avian species observed to eat fruit of *E. ngamicum*. It was common in the reserve throughout the year and was hardly ever seen close to a mistletoe plant without its feeding on the fruit. All other mistletoe-eating birds can probably be regarded as minor and incidental dispersers.

Table 1 Relative frequency (%) of records of birds feeding on fruit of mistletoes in the Loskop Dam Nature Reserve during March 1977 – April 1978

Bird species	Mistletoe species: *T. leendertziae*	*T. natalitius*	*V. combreticola*	*V. rotundifolium*	*E. ngamicum*
Speckled mousebird				X	
Redfaced mousebird	6		2		
Blackcollared barbet	4	5	2		
Acacia pied barbet	5	6	1		
Yellowfronted tinker barbet	64	80	94	X	X
Southern black tit	8	9	0,2		
Plumcoloured starling	9	X			
Redheaded weaver	3				
No. of records	409	85	665	–	–

X = recorded outside fixed observation periods.

My findings are in close agreement with Ayres's (1879) statement: 'Those [yellowfronted tinker barbets] I saw in the Transvaal were almost always on or near a species of mistletoe . . .' Dr H. Exton (quoted by Roberts 1935) also recorded mistletoe fruit as food of this species, whereas, according to Vernon (1977), it is a 'widespread resident in mixed woodland where fruit trees and the parasitic plants *Loranthus* and *Viscum* occurred' in the Zimbabwe Ruins area, Zimbabwe.

The redfaced mousebird is known to eat *V. rotundifolium* fruit (Bunning *in litt.* 1977). *Viscum verrucosum* is eaten by mousebirds (Watt & Breyer-Brandwijk 1962). Rowan (1967) reports that all South African mousebirds eat *Viscum* fruit. Whereas eating of *Viscum* fruit by mousebirds has thus been well documented, this study revealed that loranthoid fruit is also taken, at least by redfaced mousebirds. It is noteworthy that the speckled mousebird was not observed to feed on the larger *Tapinanthus* and *V. combreticola* fruit but only on the smaller *V. rotundifolium*. Though Rowan (1967) reports a wide overlap in food plants between the three South African species of mousebird, this study tends to indicate that a difference probably exists in respect of preferred mistletoe fruit in the study area. Feeding records on non-mistletoe fruit in the study area tend to corroborate this suggestion.

A blackcollared barbet in captivity ate fruit of *V. rotundifolium*. A particular pair of these birds nested close to a large *V. combreticola* without being observed to eat its fruit. This indicates that at least *V. combreticola* fruit is only incidentally taken, and that *Tapinanthus* fruits are preferred to those of *Viscum* (Table 1). Blackcollared barbets have been recorded to eat *Viscum* fruit (Anon. 1963). The eating of loranthoid fruit was observed during this study.

The acacia pied barbet has been recorded as eating *Loranthus* fruit (Anon. 1962). This was confirmed by this study for two *Tapinanthus* species. This study is the first one to record *Viscum* fruit as part of its diet. As in the case of the last species, the acacia pied barbet appears to prefer loranthoid to viscoid fruit.

This study is the first to record southern black tits, plumcoloured starlings and redheaded weavers feeding on mistletoe fruit. These species also preferred *Tapinanthus* fruit to *Viscum*. The redheaded weaver is not even recorded to eat fruit by McLachlan & Liversidge (1978). Plumcoloured starlings are summer migrants to Southern Africa. During a good fruit production season (March 1977; see Godschalk 1983a) this species fed freely on fruit of *T. leendertziae* and is probably a more important consumer of mistletoe fruit in 'good' seasons than in 'poor' seasons (Table 3).

Seasonal variation in mistletoe consumption

Considerable variation occurred in the incidence of species feeding on mistletoe fruit (Table 2), particularly in the non-tinker barbet species. This is almost completely correlated with the presence of *Tapinanthus* fruit from February to June, as non-tinker barbets ate mainly *Tapinanthus* and very few *V. combreticola* fruit (Table 1). Feeding pressure on *V. combreticola* fruit is lower during the period when *Tapinanthus* fruit is available (Figure 1). This indicates that the tinker barbet [nearly the sole consumer of the fruits of *V. combreticola* (Table 1)] shifts its mistletoe diet to *Tapinanthus* fruit when

Table 2 The number of monthly records of birds feeding on fruit of mistletoes (*T. leendertziae, T. natalitius* and *V. combreticola*) in the Loskop Dam Nature Reserve during March 1977 – April 1978 (April 1977 excluded)

Bird species	March	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April
Redfaced mousebird	21									14		5	
Blackcollared barbet	8	4								7	2	8	8
Acacia pied barbet	15	3					4				7		2
Yellowfronted tinker barbet	142	21	25	66	122	125	69	21	60	54	86	103	65
Southern black tit	36				1						4		
Plumcoloured starling	29	M	M	M	M	M					X	8	X
Redheaded weaver	14	?M	?M	?M									

?M = (probably) a summer migrant not present in study area during months indicated; X = recorded outside fixed observation periods.

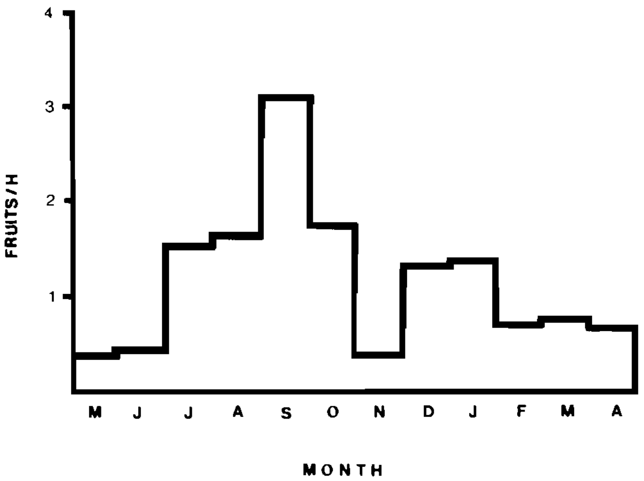

Figure 1 Rate of removal of fruit of *Viscum combreticola* by birds in the Loskop Dam Nature Reserve during May 1977 – April 1978. Based on 538 h of observations.

the latter is available, despite apparent competition by the other avian frugivores. This indicates that *Tapinanthus* is definitely preferred to *Viscum* fruit, which might be due to the presumably lower nutritional quality of *Viscum* fruit (Godschalk 1983b).

The large number of records during March 1977, particularly for the non-tinker barbets, is related to a high production of *T. leendertziae* fruit during that season (Godschalk 1983a). The records for *T. leendertziae* fruit during good (1977) and poor (1978) fruit-crop seasons are shown separately (Table 3) to illustrate different responses by mistletoe-eating birds to high and low fruit production in this species. In good crop seasons non-tinker barbets are more attracted to mistletoe fruit than in poor crop seasons. The resulting lower dispersal efficiency per mistletoe seed (see below) is probably counteracted by the actual increase in seed numbers. The increase in mistletoe eating by non-tinker barbets in a good season accentuates the opportunistic character of mistletoe fruit eating by these species in the study area.

Table 3 Relative frequency (%) of records of birds feeding on fruit of *Tapinanthus leendertziae* in the Loskop Dam Nature Reserve, during a 'good' (1977) and a 'poor' (1978) fruit production season

	Fruit production season	
Bird species	1977 ('good')	1978 ('poor')
Redfaced mousebird	9	3
Blackcollared barbet	3	6
Acacia pied barbet	6	2
Yellowfronted tinker barbet	52	81
Southern black tit	12	2
Plumcoloured starling	12	5
Redheaded weaver	6	–
No. of records	242	167

Diurnal rate and time of fruit removal

The rate at which the fruits of the three mistletoe species were removed by birds showed considerable diurnal variation (Figure 2). The overall rate of removal of fruit of *T. leendertziae* was 2,1 fruits/h (all rates of removal of fruit are per observation point). A minor peak in the birds' feeding occurred between 10h00 and 11h00 but the rate increased steadily from the lowest figure, at noon, throughout the afternoon to reach a major peak between 16h00 and 17h00. This pattern was particularly clear for the yellowfronted tinker barbet. In the other bird species no definite pattern could be observed (which applies to all three species of mistletoe) because of the variety of birds involved which were only incidental feeders on mistletoe fruit (see above).

The overall rate of removal of fruit of *T. natalitius* was low (0,4 fruits/h), which can largely be attributed to the low number of ripe fruit available on a plant simultaneously (Godschalk 1983a). The feeding records are distributed rather evenly throughout the day, except for the very low rate of removal in the early morning, and one peak between 09h00 and 10h00.

The overall rate of removal of fruits of *V. combreticola* was 1,2 fruits/h. The rate of removal during February – June, when *Tapinanthus* fruit was available, was considerably lower (0,61 fruits/h) than during the rest of the year, when only *V. combreticola* fruit was available (1,62 fruits/h, see Figure 1). The extremely high rate of removal of fruit during September might be related to the onset of the breeding season of the tinker barbet (Winterbottom 1971) when more energy would be needed for courtship, nest building and egg laying. The sharp decrease of fruit consumption during October and November might be related to an increased intake of insects for feeding of nestlings and parent birds. The parents would also need high quality food as less time would be available for foraging for their own needs. Shifting of the fledglings' diet from insects to mistletoe fruit would then restore mistletoe fruit consumption to normal levels from December onwards. The relatively low rate of removal of fruit of *V. combreticola* during February – June is largely due to the availability of *Tapinanthus* fruit during that period (see above). When *V. combreticola* was the only mistletoe fruit available (July – January), feeding pressure on its fruit was high.

The removal rates found in this study are low in comparison with some tropical fruit-bearing trees. *Cecropia peltata* trees in

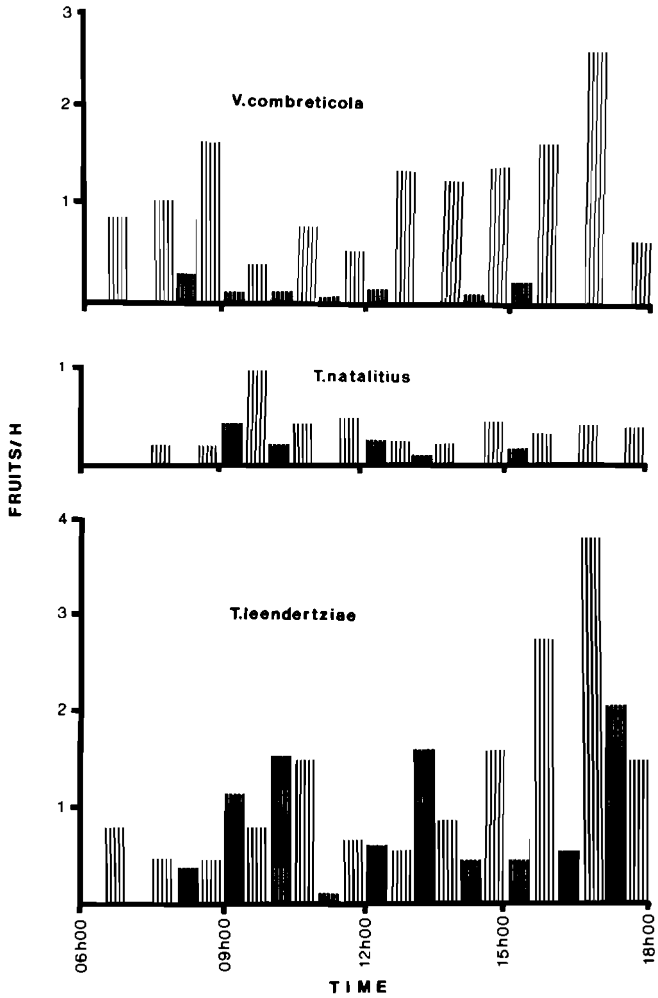

Figure 2 Diurnal variation in rate of removal of fruit of three mistletoe species by birds in the Loskop Dam Nature Reserve. Lightly shaded columns indicate records for yellowfronted tinker barbets, and heavily shaded columns records for all other bird species. Based on 198 h, 193 h and 538 h of observations on *Tapinanthus leendertziae, T. natalitius* and *Viscum combreticola*, respectively.

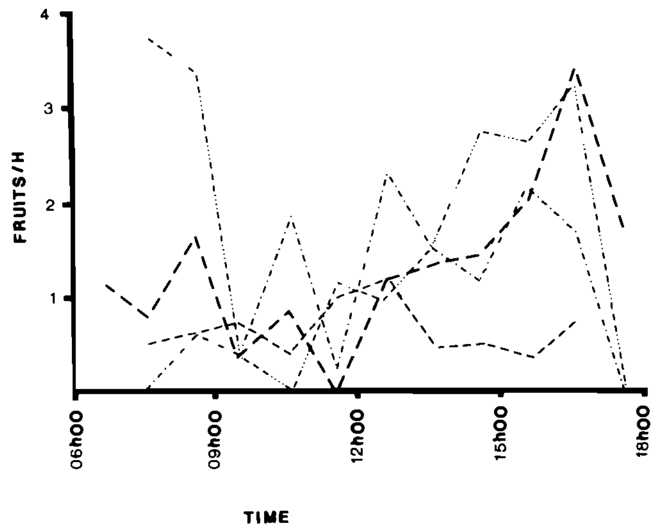

Figure 3 Diurnal variation in rate of removal of fruit of *Viscum combreticola* by birds in the Loskop Dam Nature Reserve during spring (. . . . . . _ _.; September – November), summer (_ _ _; December – February), autumn (_ _ _; March – May) and winter (_ . . . . _ ; June – August).

Jamaica were visited (which is related to fruit removal) 6,45 times/h and *Ficus trigonata* as many as 37,2 times/h (Cruz 1974).

Seasonal variation occurred in the diurnal rate of removal of fruit of *V. combreticola* (Figure 3). During autumn and winter the main consumption of fruit took place between 10h00 and 16h00. [The same pattern was observed in *T. natalitius* whose fruiting period stretched over this period (Godschalk 1983a).] This is partly related to the relatively short days and cold early mornings during this period, and probably also to the lower ambient temperatures which allow the birds to forage throughout the day without risk of heat stress. In spring (September – November), which is quite warm particularly when rains are still absent, and summer (December – February), most feeding activity occurred during the cooler early mornings and late afternoons, probably, among other things, to avoid heat stress. The same explanation probably pertains largely to the pattern observed for *T. leendertziae*. It may be mentioned that in this specific season (1977/78) the mean maximum temperature during the spring was even higher (29,3°C) than that during the summer (29,2°C).

The major peak in the rate of removal of fruit of *T. leendertziae* and *V. combreticola* during the late afternoon (higher than the morning peak) is interpreted as increased feeding to obtain food for the long night ahead (about 10 – 12 h during which no feeding is possible). The even distribution of the rate of removal of *T. natalitius* fruit is probably related to the relatively low number of fruit available at any one plant (Godschalk 1983a). As fruits were taken at a steady rate throughout the day, insufficient fruit would probably be left towards the end of the day to permit an increase in the rate of removal.

The overall rates of removal of mistletoe fruit by birds appear to be related to the number of fruits simultaneously available on a plant. During the exceptionally good fruit crop of *T. leendertziae* during March 1977 (Godschalk 1983a), the rate of removal of its fruit was as high as 3,2 fruits/h, whereas during the poorer 1978 season it was 1,4 fruits/h. The rate of removal of fruit of *T. natalitius*, which has few fruit simultaneously available per plant (Godschalk 1983a), was only 0,4 fruits/h, and for *V. combreticola*, with a moderate number of fruit available simultaneously, it was 1,2 fruits/h.

Handling methods

Birds were observed to deal with the various parts of mistletoe fruit in three main ways. Seeds were either directly deposited on a branch (pecking method) or swallowed. Birds that swallowed seeds either regurgitated them afterwards or defaecated the seeds. Each of these methods has its own effects on seed dispersal.

The two barbet species, the tinker barbet and the starling, which together were responsible for the consumption of between 82% and 97% of the mistletoe fruit concerned, regurgitated the seeds shortly after swallowing (see below) the seeds and fleshy layers. The regurgitated seeds were always without the fleshy layer immediately surrounding the seeds. Because of their stickiness the seeds stuck to the beak of the bird and were subsequently wiped off onto the branch to which they invariably adhered firmly.

Regurgitation of mistletoe seeds in Afrotropical birds has formerly been reported in redfronted *Pogoniulus pusillus* and goldenrumped *P. bilineatus* tinker barbets in Natal (Cowles 1959; Frost 1980), moustached green tinker barbets (*P. leucomystax*) in Malawi (Dowsett-Lemaire 1982), and the crested barbet in captivity (Godschalk 1976). Regurgitation of mistletoe seeds is apparently rather rare in other continents and has only been reported for a redeyed vireo *Vireo olivaceus* in Jamaica (Gosse 1847, quoted in Ridley 1930), several tyrant flycatchers (Family Tyrannidae) in Panama (Leck 1972; Davidar 1983), the whitecheeked cotinga *Zaratornis stresemanni* in Peru (Parker 1981) and the grey currawong *Strepera versicolor* in Australia (Brittlebank 1908). The currawong, however, cast the seeds together with other food remains in the form of pellets, making them unsuitable for effective dispersal.

The mousebirds were observed to defaecate *Viscum* seeds and, based on strings of defaecated *Tapinanthus* seeds in the field, were suspected to defaecate the latter, too. Unlike the previous group of birds, mousebirds consumed *Viscum* fruits whole. The seeds were defaecated in clumps just dropped to the ground. Clumps adhering to branches usually formed long strings down from the branch with only one or two seeds in close contact with the branch. Captive blackeyed bulbuls, kurrichane and olive *Turdus olivaceus* thrushes, and Cape white-eyes all defaecated the seeds when fed fruit of *V. rotundifolium* (Godschalk 1976). The defaecation of mistletoe seeds has been reported from all continents in a wide variety of birds (see Godschalk 1979).

Southern black tits and redheaded weavers did not swallow *Tapinanthus* seeds but, after discarding the exocarp, deposited the content of the fruit onto the branch on which they were sitting. Most of the fleshy layer was pecked off leaving the seed adhering to the branch. The adhesion was not always firm because not all of the fleshy layer had been removed. Similar behaviour, performed by birds while eating mistletoe fruit, has been described only for the blackcap *Sylvia atricapilla* feeding on *V. album* fruit in France (Heim de Balsac & Mayaud 1930), which ate both the exocarps and the fleshy layer (pulp) leaving the seed attached to the branch.

The process, mentioned in the South African botanical literature (Marloth 1913; Stoneman 1915; Letty 1962; Batten & Bokelman 1966; Compton 1966; Van Hoepen 1968), whereby the seed is wiped off the beak during handling of the fruit, was not observed during this study. As these references are not substantiated by detailed descriptions, it is not clear how many of them refer to the wiping of the seed off the beak after regurgitation. It is possible, because of the viscous layer around the seed, that sometimes a mistletoe fruit will stick to the bird's beak while the bird is feeding, and will be wiped off, but this will only occur incidentally and was never observed during this study despite extended periods of detailed observation. It is unlikely that birds will regularly fly around with these seeds stuck to their beaks, and deposit the seeds far from the parent plant as suggested by Van Hoepen (1968).

Size of feeds and duration of visits

A feed was defined as the number of fruits taken consecutively before the birds started regurgitating the seeds. The mean size of feeds varied with mistletoe species and frugivore species concerned (Table 4). The size of feeds in captive tinker barbets was similar to that found in the field, whereas a captive blackcollared barbet occasionally consumed up to seven seeds of *V. combreticola*.

The number of fruits per feed seems to be related to the size of the bird, as well as to the size of the seeds involved. The smallest number of fruits per feed was usually taken by the tinker barbet (Table 4) which was the smallest mistletoe fruit eater. On the other hand, the largest bird involved, the starling, took the largest number of fruit per feed. As the seeds of a particular feed are regurgitated quickly after each other (see next section) and, because of the sedentary behaviour of

Table 4 The number of fruits of three mistletoe species taken per feed by four species of birds in the Loskop Dam Nature Reserve

	Species of mistletoe		
Species of birds	*T. leendertziae* mean (range; *N*)	*T. natalitius* mean (range; *N*)	*V. combreticola* mean (range; *N*)
Blackcollared barbet	2,6(2 – 4; 5)	2,0(1 – 3; 4)	3,8(3 – 4; 4)
Acacia pied barbet	3,2(2 – 4; 6)	2,0(2; 1)	3,0(3; 1)
Yellowfronted tinker barbet	1,9(1 – 3; 102)	1,6(1 – 3; 28)	3,2(1 – 5; 65)
Plumcoloured starling	4,5(1 – 8; 13)	–	–

birds while regurgitating a set of seeds, it is likely that seeds derived from any particular feed, will be deposited closer to each other than seeds of different feeds. Therefore, larger feed sizes will lead to more clustered deposition of seeds resulting in more severe competition between propagules. In this respect, the tinker barbet is the most effective disperser of the four avian species which regurgitate the seeds.

The feeds involving fruit of *T. natalitius* (which has the largest seeds) were smallest, whereas those involving fruit of *V. combreticola* (which has the smallest seeds) were largest (Table 4). This is probably a function of the limiting capacity of the birds' stomachs. Because larger feed sizes lead to more clustered seed deposition (see above), seeds of *V. combreticola* are probably deposited more clustered, which agrees with field observations on large clusters of seeds and plants of this species. Clustered deposits of *Tapinanthus* seeds, on the other hand, were found infrequently in the field. The number of fruits per feed hardly influenced the amount of time spent by the tinker barbet on 'handling' individual fruits (see below) and thus did not affect 'handling' efficiency.

The mean duration of visits of the tinker barbet to plants of *T. natalitius* was 2,2 min (range 1 – 6 min, $n = 14$) and in the case of *T. leendertziae* it was 3,1 min (range 1 – 10 min, $n = 19$). During these visits they were never observed to eat more than eight fruits per visit. In contrast, the mean duration of visits to *V. combreticola* was 12,1 min (range 1 – 57 min, $n = 30$) during which as many as 40 fruits were consumed. In the last-mentioned species the length of the visits contributed substantially to the clustered deposition of its seeds.

There appears to be no direct relation between the number of ripe fruit available on the plants of a species and the duration of bird visits to these plants. Admittedly, the shortest visits were paid to *T. natalitius* plants which have the lowest number of fruit available simultaneously. In the case of *T. leendertziae* with its large amounts of ripe fruit available, however, tinker barbets usually terminated their visits after feeding on a few fruits of plants full of ripe fruit. The rate of removal of *T. leendertziae* fruits was, however, highest, indicating that the birds moved around more between visits to *T. leendertziae* plants than to *V. combreticola* plants. This may partly be because a certain proportion [e.g. 32% of the plants involved in a phenological survey (Godschalk 1983a)] of *V. combreticola* plants are male individuals which do not bear fruit at all, presumably resulting in a lower number of fruit-bearing plants in an area. This would force a bird to pay relatively long visits to single plants. The suggested lower nutritional value of *V. combreticola* fruit compared to those of *T. leendertziae* (Godschalk 1983b) would make it energetically less rewarding to pay short visits to this food resource of lower nutritional quality, but would rather force the bird to exploit this resource without wasting energy in moving around.

A few observations are available for those avian species which do not regurgitate seeds. Once a redfaced mousebird was observed to consume 10 fruits of *T. leendertziae* within 3 min, which gives an indication of the bird's food-storing capacity. Flocks of mousebirds sometimes spent long periods feeding and resting on mistletoe plants, resulting in many seeds being defaecated on, under or close to the parent plants. The tits and weavers usually departed after feeding on at most five fruits.

Duration of the components of the handling process

'Handling time' was defined as the time lapse between the swallowing of the first fruit and the depositing of the last seed divided by the number of fruits taken per feed. The mean duration of the different components of the handling process of mistletoe seeds differed markedly between frugivore species and between mistletoe species (Table 5). The tinker barbet was the most efficient mistletoe fruit eater handling fruit of *T. leendertziae* and *V. combreticola* faster than either of the other two barbet species. It handled fruit of *T. natalitius* faster than the blackcollared barbet, but apparently more slowly than the acacia pied barbet. This may, however, be a wrong impression, since the data for the latter species are not sufficiently representative. The starling had a speed of handling fruit of *T. leendertziae* similar to that of the tinker barbet, mainly because of the fast rate of consumption (component 1). This might be attributed to its larger size enabling it to take a whole feed without any need to move. The handling time per fruit was inversely related to the size of the seed involved. Fruit of *T. natalitius*, having the largest seed, was handled slowest, whereas fruit of *V. combreticola*, with the smallest seed, was handled fastest. The proportionally very slow speed of handling fruit of *T. natalitius* (Table 5) is probably bound up with the tough pellicle (fleshy layer), which is more difficult to remove than the fragile fleshy layer of *T. leendertziae* (Godschalk 1983c). In the case of *V. combreticola*, the small size of the seed as well as the jelly-like nature of its fleshy layer (Godschalk 1983c) probably facilitate fast handling. The relatively high speed of handling mistletoe seeds (between 30 – 60 s/seed) suggests that the fleshy layer is removed mechanically, presumably in the stomach.

Handling time per fruit in the tinker barbet is possibly slightly reduced if only one fruit is taken per feed (Table 6), but otherwise variation in the size of the feed has virtually

Table 5 Mean duration (s) of different components of the feeding process of fruit of three mistletoe species by four species of birds which regurgitate seeds, in the Loskop Dam Nature Reserve

Bird species	Mistletoe species	Component 1 mean (range; *N*)	Component 2 mean (range; *N*)	Component 3 mean (range; *N*)
Blackcollared barbet	T.l.	26,0(19 – 37; 5)	39,0(31 – 47; 2)	34,5(29 – 45; 4)
	T.n.	30,0(22 – 38; 2)	77,7(45 – 120; 3)	36,0(28 – 40; 3)
	V.c.	13,9(7 – 22; 8)	35,0(35; 1)	26,7(19 – 36; 3)
Acacia pied barbet	T.l.	26,5(21 – 33; 4)	37,0(35 – 41; 3)	38,6(10 – 90; 10)
	T.n.	19,0(19; 1)	43,0(43; 1)	31,0(31; 1)
	V.c.	17,0(12 – 22; 2)	31,0(31; 1)	25,0(18 – 32; 2)
Yellowfronted tinker barbet	T.l.	16,7(6 – 31; 47)	36,4(18 – 100; 37)	21,6(10 – 43; 34)
	T.n.	18,4(14 – 29; 9)	58,2(26 – 153; 11)	43,4(16 – 115; 5)
	V.c.	14,4(3 – 32; 103)	22,8(12 – 48; 44)	19,1(5 – 53; 95)
Plumcoloured starling	T.l.	9,3(5 – 13; 15)	48,8(35 – 60; 4)	21,9(5 – 50; 26)

T.l. = *Tapinanthus leendertziae*; T.n. = *T. natalitius*; V.c. = *Viscum combreticola*.
Component 1 = interval between swallowing of consecutive fruits in a feed; Component 2 = interval between swallowing of the last fruit in a feed, and regurgitation of the first seed; Component 3 = interval between regurgitation of consecutive seeds in a feed.

Table 6 Mean duration (s) of different components of the handling procedure of fruit of three mistletoe species by the yellowfronted tinker barbet in relation to the number of fruits per feed (see Table 5 for definitions of components 1 – 3)

Mistletoe species	No. fruits per feed	Component 1 mean (*N*)	Component 2 mean (*N*)	Component 3 mean (*N*)	Mean handling time/fruit
T. leendertziae	1	–	33,4(12)	–	33,4
	2	18,3(27)	37,8(19)	21,5(20)	38,8
	3	14,7(20)	40,3(6)	21,6(14)	37,6
T. natalitius	1	–	57,0(6)	–	57,0
	2	15,8(5)	49,3(4)	60,0(3)	62,6
	3	21,3(4)	101,0(1)	18,5(2)	60,2
V. combreticola	1	–	24,5(2)	–	24,5
	2	13,7(15)	25,3(12)	20,4(9)	29,7
	3	14,7(22)	19,7(10)	20,4(16)	30,0
	4	15,5(41)	22,7(15)	17,7(43)	30,6
	5	12,1(16)	23,0(3)	20,1(16)	30,4

no influence on the speed at which individual fruits are handled.

The retention times of regurgitated mistletoe seeds reported in this study are very much shorter than any published formerly. The whitecheeked cotinga in Peru regurgitated mistletoe seeds 5 – 10 min after swallowing them (Parker 1981). In South Africa, the crowned hornbill *Tockus alboterminatus* regurgitated seeds of several plant species within half an hour (Ranger 1950) and several migratory bird species in Panama took 5 – 20 min to regurgitate seeds of *Guarea glabra* (Howe & De Steven 1979).

The short retention time of mistletoe seeds in the guts of birds which regurgitate the seeds points to potentially fast rates of removal of fruit (in the tinker barbet approximately 90 fruits/h for *T. leendertziae*, 60 fruits/h for *T. natalitius* and 120 fruits/h for *V. combreticola*). The roughly approximated number of fruits of *T. leendertziae* needed to satisfy the daily energy requirements of the yellowfronted tinker barbet (172 fruits/day, see Godschalk 1983b), could be consumed in 2 h of continuous feeding.

The processing time of fruit of *T. leendertziae* by the tits averages 27,7 s/fruit (20 – 38 s; $n = 9$); in the weaver it was 45 s/fruit. The time lapse between swallowing and defaecation of mistletoe seeds by mousebirds could not be measured in the field. During the present study as well as during a pilot project (Godschalk 1976) data were obtained on several captive frugivorous bird species (Table 7). These data are roughly similar to those reported in other regions, except for the much shorter time reported for the oriental *Dicaeum* species (Table 7), which have a highly specialized intestinal structure causing mistletoe seeds to by-pass the gizzard and enter the intestine from the oesophagus directly (Dammerman 1929; Desselberger 1931; Mayr & Amadon 1947; Docters van Leeuwen 1954). This results in an extremely short retention time of mistletoe seeds in these birds.

Interaction between birds feeding on mistletoe fruit

No interspecific aggression between birds feeding on mistletoe fruit was observed. At *T. leendertziae* plants the tinker barbet was once observed feeding in association with redfaced mousebirds, a pied barbet and a plumcoloured starling respectively, and twice with blackcollared barbets. At *T. natalitius* plants tinker barbets were observed once in association with tits. At *V. combreticola* plants tinker barbets were never observed in associaton with other mistletoe-eating frugivores. The number of interspecific associations at different mistletoe species correlates well with the pattern of consumption of the fruit of these species (see above).

Intraspecific aggression was observed only in the tinker barbets. Individual tinker barbets normally fed alone but never more than two together. During nine of the 14 observed occasions of two-bird associations, intraspecific aggression

Table 7 Time lapse between swallowing and defaecation of mistletoe seeds by various avian frugivores

Bird species	Mistletoe species	Time lapse (min) mean (range; *N*)	Source
Afrotropical region			
Blackcollared barbet	*V. combreticola*	22(10 – 35; 10)	Present study
Blackcollared barbet	*V. rotundifolium*	24(18 – 33; 6)	Present study
Crested barbet	*V. rotundifolium*	17,7(8 – 38; 78)	Godschalk (1976)
Blackeyed bulbul	*V. rotundifolium*	18,5(5 – 34; 128)	Godschalk (1976)
Kurrichane thrush	*V. rotundifolium*	23(23; 6)	Godschalk (1976)
Oriental region			
Tickell's flowerpecker (*Dicaeum erythrorhynchos*)	*Dendrophtoe falcata*	3 – 4	Ali (1931)
	Loranthus longiflorus	8 – 12	Ryan (1899; quoted by Docters Van Leeuwen (1954))
Javan firebreasted flowerpecker (*D. sanguinolentum*)	*Macrosolen cochinchirensis*	17(12 – 22; 6)	Docters Van Leeuwen (1954)
	Scurrula atropurpurea	22(22; 3)	Docters Van Leeuwen (1954)
Australian region			
Swallow mistletoebird (*D. hirundinaceum*)	*Amyema gaudichaudii* *A. miquelli*	25 – 60	Keast (1958)
Australian silvereye (*Zosterops lateralis*)	*Amyema gaudichaudii* *A. miquelii*	30 – 80	Keast (1958)
Nearctic region			
Phainopepla (*Phainopepla nitens*)	*Phoradendron californicum*	29(12 – 45)	Walsberg (1975)
Palearctic region			
Mistle thrush (*Turdus viscivorus*)	*V. album*	30	Tubeuf 1923, (quoted by Kuijt (1969))
Bohemian waxwing (*Bombycilla garrulus*)	*V. album*	6 – 31	Borowski (1966)

occurred (Table 8). The proportion of aggressive encounters as a function of two-bird associations did not differ significantly between the three mistletoe species. The number of two-bird associations, and consequently of intraspecific aggressive encounters, seems to be inversely related to the duration of visits to plants of different mistletoe species (see above). Shorter visits are presumably related to more wandering about which increases the change of encounters. On two occasions a tinker barbet was observed to feed mistletoe fruit to its associate; on one of the occasions the associate was definitely a female fed by a male, because copulation followed.

Intraspecific aggressive encounters of tinker barbets at mistletoe plants were recorded from March to October and were thus not tied up with the breeding cycle [September to December in Transvaal (Winterbottom 1971)]. Furthermore, tinker barbets reacted vigorously to playback of their calls throughout the year. The above findings suggest that pairs of yellowfronted tinker barbets maintain territories throughout the year within which they *inter alia* may obtain their food, and from which they exclude conspecifics. Mistletoe plants may be important focal points within these territories. Nothing has been published on possible territoriality in tinker barbets.

The number of intra- and interspecific associations at mistletoe plants observed during this study is very low compared to those in some tropical situations where a fruiting tree may be visited by as many as 28 birds of 15 species simultaneously (Cruz 1974) and where interspecific competition at fruiting trees is sometimes severe (Howe 1981). This is probably mainly related to the low visitation rates to southern African mistletoes (see above).

Post-feeding behaviour

A comparison of the sites at which seeds of the three mistletoe species were deposited, is presented in Table 9. Forty-seven per cent of the seeds of *T. natalitius*, 42% of those of *T. leendertziae* and only 17% of those of *V. combreticola* were carried away from the parent plants. For the tinker barbet alone the corresponding figures were 61, 50 and 15%, respectively. The proportion of seeds carried away was inversely related to the duration of the birds' visits (see above) and the retention time of the seeds (see above). During long visits most seeds were regurgitated on the parent plant, and only seeds ingested during the last feed were carried away. A short retention time of seeds resulted in relatively more seeds being deposited on the parent plant. These two factors, combined, resulted in a relatively high proportion of seeds of *V. combreticola* being wasted through deposition on the parent plant or its host. In *T. natalitius*, however, a higher proportion of seeds was carried away from the parent plant, because bird visits were shortest and seeds were retained longest (see above). Only 19% of the seeds were carried away when the pecking method of feeding was used, showing the relative inefficiency of this method for seed dispersal.

The proportion of mistletoe seeds carried away from the parent plant found in this study compares unfavourably with situations in central America where 62% of the seed of a Panaman nutmeg *Virola surinamensis* were removed from parent plants (Howe & Vande Kerckhove 1980). In *V. sebifera* this figure was found to be as high as 85% (Howe 1981).

The mean distance of the birds' immediate, post-feeding flights away from mistletoe plants is presented in Table 10. Most flights were shorter than 50 m while very few exceeded 100 m. If the distances of post-feeding flights are considered to be good approximations of the distances at which not-yet-voided seeds were deposited (which, in view of the short retention time, is reasonable), then seed dispersal apparently occurs not far from the parent plants.

No relation was found between the distance of post-feeding flights of the tinker barbets and either the number of trees (Figure 4), or the number of fruit-bearing mistletoe plants (Figure 5) in the area around the plant at which the bird had been feeding.

Several factors may influence the post-feeding behaviour of birds, including their nutritional and reproductive state, the size of their territory (if a territory is held), the distance to nesting site (if breeding) and weather conditions (Labitte 1952).

Mousebirds sometimes remained on a mistletoe plant for relatively long periods, resulting in many seeds being deposited near the parent plant. On other occasions, however, they made relatively long post-feeding flights. Tubeuf (1923, quoted by Scharpf & McCartney 1975) found that the maximum distance

Table 8 Intraspecific aggressive interactions of yellowfronted tinker barbets at mistletoe plants

Mistletoe species	No. two-bird associations	No. aggressive interactions
T. leendertziae	3	2
T. natalitius	9	6
V. combreticola	2	1
Total	14	9

Table 9 Number of seeds of three mistletoe species deposited either on the parent plant and its host (H) or on other potential hosts (O), after regurgitation, or deposition of the seed during 'pecking', by birds in the Loskop Dam Nature Reserve

	Mistletoe species					
	T. leendertziae		*T. natalitius*		*V. combreticola*	
Bird species	H	O	H	O	H	O
Blackcollared barbet	9	4	11	–	4	11
Acacia pied barbet	10	11	–	2	3	–
Yellowfronted tinker barbet	100	98	21	33	342	61
Southern black tit	13	8	8	–	–	1
Plumcoloured starling	39	11				
Redheaded weaver	14	–				
Total	185	132	40	35	349	73

Table 10 Distance (m) of post-feeding flights of birds from plants of three mistletoe species in the Loskop Dam Nature Reserve

Bird species	*T. leendertziae* mean (range; *N*)	*T. natalitius* mean (range; *N*)	*V. combreticola* mean (range; *N*)
Blackcollared barbet	35,0(30 – 40; 2)		36,7(20 – 50; 3)
Acacia pied barbet	5,0(5; 2)	15,0(15; 1)	
Yellowfronted tinker barbet	19,8(3 – 50; 37)	24,6(5 – >50; 7)[b]	34,2(4 – 75; 26)
Southern black tit	4,5(2 – 7; 2)		20,0(20; 1)
Plumcoloured starling	68,3(5 – >100; 3)[a]		

[a] > 100 m substituted by 150 m; [b] > 50 m substituted by 75 m
The difference between the distance of the flights from the three mistletoe species by yellowfronted tinker barbets was not significant ($t_{calc.} = 0,72$; $t_{0,975} = 2,05$; for the comparison between *T. leendertziae* and *V. combreticola*)

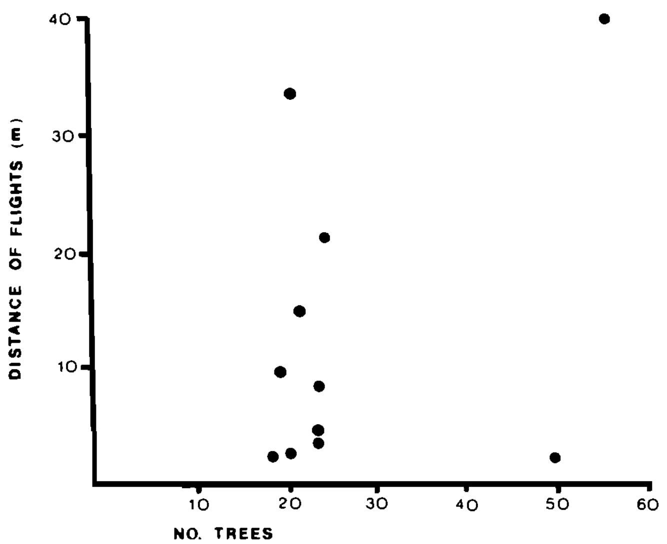

Figure 4 Relation between distance of post-feeding flights of yellowfronted tinker barbets from individual mistletoe plants, and the number of trees within a radius of 20 m of those individuals. Each dot represents the mean distance recorded at each of 11 observation sites. (The function of the regression line derived from these data, is: $f(x) = 0,7883 + 0,0554x$. The fit was, however, very weak ($\chi^2_{calc.} = 116,93$; $\chi^2_{0,05;\ 10} = 3,94$) so that there is apparently no direct relation between the characters represented by the x and y axes).

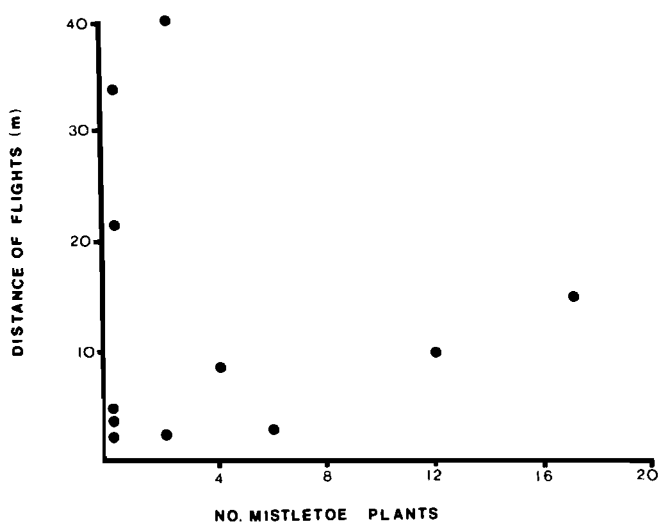

Figure 5 Relation between distance of post-feeding flights of yellowfronted tinker barbets from individual mistletoe plants and the number of fruit-bearing mistletoe plants within a radius of 20 m from those individuals. Each dot represents the mean distance recorded at each of 11 observation sites. (The function of the regression line derived from these data, is: $f(x) = 9,8717 - 0,4488x$. The fit was, however, very weak ($\chi^2_{calc.} = 276,89$; $\chi^2_{0,05;\ 10} = 3,94$), so that there is apparently no direct relation between the characters represented by the x and y axes.

over which the mistle trush *Turdus viscivorus* (which also defaecates mistletoe seeds) actually carried seeds away from the parent plant, was 'less than one mile.'

Conclusions

Both in terms of quality and quantity of mistletoe seed dispersal the yellowfronted tinker barbet must be regarded as the main and most important single disperser of seeds of the three mistletoes involved in this study in the study area. All other mistletoe fruit consumers were relatively unimportant. This pattern is probably true over the whole distribution range of tinker barbets (Godschalk 1983d), particularly for the larger fruited mistletoes. However, the pattern for the small-fruited *V. rotundifolium* might be quite different. Existing information (Godschalk 1983c) indicated that smaller fruited *Viscum* species are dispersed by a wider variety of birds than larger fruited ones.

The three mistletoe species under discussion differ in their degree of dependency on the yellowfronted tinker barbet for their seed dispersal (Table 1), though this bird is still the main dispersal agent of all these species. These differences, possible reasons for them and their implications are discussed in a broader context elsewhere (Godschalk 1983d).

The regurgitation technique is the most efficient seed dispersal technique of those employed by mistletoe-eating birds. This technique is used by several species of birds which, together, are responsible for the consumption of between 82% and 97% of the fruit of the mistletoe species under consideration. For the birds it offers the highest food reward per unit time and unnecessary extra energy-demanding ballast is carried around for only a very short period of time. For the plants, it ensures the secure deposition on a branch of almost all seeds handled in this way. This is of utmost importance to mistletoes as all seeds not deposited securely on a host branch are completely wasted. Major disadvantages of this technique are the high proportion of seeds deposited on the parent plant of its host, and the relatively short distance the remaining seeds are carried away.

The defaecation technique is used in the case of only 0 – 6% of the mistletoe seeds. This technique leads to a large wastage of seeds through largely improper and clustered deposition of the seeds, or loss to the ground. It is, however, probably important for long-distance dispersal, as the seeds are retained much longer in the bird's alimentary tract. Mousebirds may be particularly important in this respect because of their sometimes relatively long post-feeding flights and greater mobility (Pocock 1966). The defaecation technique is probably also more important for the dispersal of the smaller seeded *Viscum* species like *V. capense* and *V. rotundifolium*, the fruit of which are consumed by a wider variety of generalist frugivores (Godschalk 1983c).

The pecking technique is not very efficient as a dispersal mechanism for mistletoe seeds and can be considered of only minor and very local significance. This study showed that the feeding behaviour of mistletoe-eating birds forms a most important part of the dispersal strategy of southern African mistletoes (Godschalk 1983d).

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Appendix 1 Frugivorous birds (according to McLachlan & Liversidge 1978) observed within 40 m of mistletoe plants in the Loskop Dam Nature Reserve, South Africa, with an indication of their relative abundance (according to Baker 1970)

	Relative abundance
Redeyed dove, *Streptopelia semitorquata*	A
Green pigeon, *Treron calva*	UC
Grey loerie, *Corythaixoides concolor*	UC
Speckled mousebird, *Colius striatus*	VC
Redfaced mousebird, *C. indicus*	UC
Grey hornbill, *Tockus nasutus*	C
Yellowbilled hornbill, *T. flavirostris*	UC
Blackcollared barbet, *Lybius torquatus*	FC
Acacia pied barbet, *L. leucomelas*	R
Yellowfronted tinker barbet, *Pogoniulus chrysoconus*	VC
Crested barbet, *Trachyphonus vaillantii*	C
Black cuckooshrike, *Campephaga flava*	FC
Blackheaded oriole, *Oriolus larvatus*	FC
Southern black tit, *Parus niger*	VC
Arrowmarked babbler, *Turdoides jardineii*	VC
Blackeyed bulbul, *Pycnonotus barbatus*	A
Kurrichane thrush, *Turdus libonyana*	VC
Cape robin, *Cossypha caffra*	C
Chestnutvented titbabbler, *Parisoma subcaeruleum*	UC
Plumcoloured starling, *Cinnyricinclus leucogaster*	C
Cape glossy starling, *Lamprotornis nitens*	C
Redwinged starling, *Onychognathus morio*	VC
Cape white-eye, *Zosterops pallidus*	VC
Redheaded weaver, *Anaplectes rubriceps*	(1)
Cape weaver, *Ploceus capensis*	(2)
Masked weaver, *P. velatus*	VC
Yellow-eye canary, *Serinus mozambicus*	A

A = abundant; VC = very common; FC = fairly common; C = common; UC = uncommon; R = rare.
(1) no recent records in the area according to Baker (1970), but recorded during this study (Godschalk 1981); probably rare.
(2) not recorded by Baker (1970) but observed during this study (Godschalk 1981); probably rare.