HOME RANGE AND EXTRA-COURT ACTIVITY IN THE MALE TOOTH-BILLED BOWERBIRD, *SCENOPOEETES DENTIROSTRIS* (PTILONORHYNCHIDAE).

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Home range, time utilisation and activities of four male Tooth-billed Bowerbirds away from their adjacent courts were monitored by radio-tracking throughout the 1989 display season in upland rainforest of north Queensland. Three of the males were known to be adults, having attended their courts for ten or more seasons. Males spent an average of 36% of their time absent from courts during peak display season activity. The mean home range of males was 9.5ha, with a mean overlap of 50%. Median distances travelled by males from their courts for all activities ranged from 40-86m, with a maximum range of 311-391m. Activities away from courts included foraging, collection of leaf decorations directly from trees or by theft from neighbouring courts, interactions with conspecifics, bathing and drinking. Most absences (60%) were primarily for foraging which represented 83% of total time absent with a mean duration of 18mins per absence. Some 18% of absences, representing 7% of total time absent, involved exclusive non-foraging activities. Almost all of these absences were brief with a mean duration of 5 mins. The remaining 22% of absences, representing 10% of total time absent, from the court involved unknown activities. Absences from courts were shortest during November, and during the early part of the morning (0600-0900h). The implications of these data are discussed. □ *Tooth-billed Bowerbird home range size, time utilisation and activities away from courts, Ptilonorhynchidae, Australia.*

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Several families of passerine birds include species that exhibit polygynous mating systems in which promiscuous, competitive and often ornate males take no part in nest duties. In most of these species males spend much of the day at either solitary or communal (lek) display perches; females are attracted to these sites by the calls of the males and are courted by a variety of displays (Gilliard, 1969; Snow, 1982; Beehler & Pruett-Jones, 1983, Beehler 1989). The Tooth-billed Bowerbird, *Scenopoeetes dentirostris* is one such species (Frith & Frith, 1985, 1993). Males of this species establish cleared courts on the forest floor in areas of suitable topography; mean nearest neighbour distances in these areas are 50m (Frith & Frith, in press). Frith and Frith (1994) found that during peak activity male Tooth-bills spent an average of 64% of the day (0600-1800h) at courts; court visits averaged 23mins and court absences averaged 14mins. The birds spent more time at their courts during seasons of greater fruit abundance.

The behaviour of male Tooth-bills at courts is increasingly well understood (Frith & Frith, 1993, 1994; in press). However, nothing is known about home range size, time utilisation and activities of male Tooth-bills away from their courts. This paper reports observations on the behaviour and movement of four court-owning male Tooth-bills using radio-tracking and simultaneous observation from hides near courts. The aims of this work were threefold: to identify the role of male Tooth-bills as seed dispersers within tropical rainforest (Moore, 1991); to determine whether male Tooth-bills spent much time present, but silent, in the canopy above or within the vicinity of their court (Frith & Frith 1994); and to ascertain home ranges and activities of males away from the courts. The third aim is the subject of the present paper.

STUDY AREA AND METHODS

The study area comprised 50ha of upland tropical rainforest, altitude c.875m, on the Paluma Range (19°00'S, 146°10'E), north-eastern Queensland, 7km from Paluma Township, 80km north of Townsville. Descriptions of the Paluma Range study area and its climate appear in Frith and Frith (1994). Half of the site was divided into permanently marked 25 × 25m grid squares and

the remainder was divided into 25 × 50m rectangles; this enabled accurate plotting of locations at which the birds were observed.

Radio-tracking was undertaken during the 1989 display season (17-27 October, 16-26 November and 12-22 December). Four males (from courts 23, 33, 35, 37; Frith & Frith, 1994: fig. 1) were caught in mist nets near their courts and were banded with a metal band and a unique two colour-band combination. Males at courts 23 and 37 had been the traditional owners at those sites for ten previous display seasons and the male at court 35 for 11 previous seasons. The male at site 33 was unbanded at the start of the 89 display season and may have been the unmarked owner of this site for the two previous seasons.

Each male was monitored for four periods (0600-0900, 0900-1200, 1200-1500, 1500-1800h) during October, but only three males were monitored during November (at sites 23, 35, 37) and December (23, 33, 37). All males were radio-tracked for a total of 120 hours. The first hour of the first tracking period (at site 33) was excluded from the analysis due to possible disturbance (see below). Male 37 lost a transmitter during one tracking period and, although his court arrivals and departures were recorded, his activities away from the court were unknown. Radio-tracking was also carried out after 2000h, for two 30 minute periods at each court, to ascertain whether the owner roosted above his court.

Each male was fitted with a 4g Biotrack single stage radio-transmitter (SS-1) using a tail mount (Kenward, 1978). Radio-tagged individuals were readily identified by the antenna extending beyond the tail. To assist rapid identification of individuals when they were in the canopy a small amount of contrasting-coloured paint was placed on the underside tips of the outer tail feathers. Radio-tracking was initiated a week after capture to allow sufficient time for the birds to adjust to the transmitter.

We established cryptic canvas hides six metres from each court two weeks before starting the study. The observer (DWF) remained within the hide during each tracking period and all bird behaviour, locations, departure and return times and flight directions were noted. Each three hour observation period was started either ten minutes after establishing DWF in the hide or earlier if the male returned to his court and behaved normally. The observer was in constant radio contact with the radio-tracking team and alerted them as soon a bird left or arrived at his court.

The radio-tracking team remained at least 30m distant from the courts of the radio-tagged birds to minimize disturbance to the court owner or to other Tooth-bills in the area. The tracking team consisted of GJM, with the radio antenna and receiver, who followed the bird's signal and marked destinations, and CBF who attempted to maintain visual contact with the bird and informed GJM of its location and behaviour in the canopy and of the compass bearing of signals.

Males were tracked using a Telonics (U.S.A.) Tr-2 receiver. To improve reception at close range and direction finding ability, an enhanced manual gain control was fitted to the reciever. A three element, folding hand held Yagi antenna (Custom Electronics, U.S.A.) was used for direction finding. Use of a small single earphone assisted communication between observer and tracker; this was necessary because many forays resulted in a dash of up to 400m to determine the bird's destination.

Once a male had been followed to a destination, the tree was tagged and, at a later date, the positions of all destination trees were mapped in relation to the pre-established grid. On a few occasions males flew beyond the limits of the study site; in these cases the locations of destination trees were plotted by tape and compass.

Signal strength and consistency were used as a guide to bird activity and if the bird could not be sighted, its position was determined by triangulation. If the signal was strong and consistent, this usually meant the bird was stationary. A bearing was then taken from the nearest grid reference point and a second bearing taken at the next grid reference point to obtain a fix. To test the accuracy of this method, calibration transmitters were placed in trees and the resulting fixes were found to be within 5m of the actual transmitter position.

A highly variable signal, in both strength and consistency, indicated the bird was moving. In these cases the signal was followed until a strong and consistent signal was obtained and the process was then repeated. If foraging, a strong variable signal was obtained as the bird would change its orientation while moving between branches. The sound of falling debris or fruit was often a good indicator of approximate bird location within the forest canopy. If interacting with other individuals, calls and chase flights were often heard.

Establishing a final destination using radio-assisted surveillance usually resulted in tracker and observer reaching a destination some time after

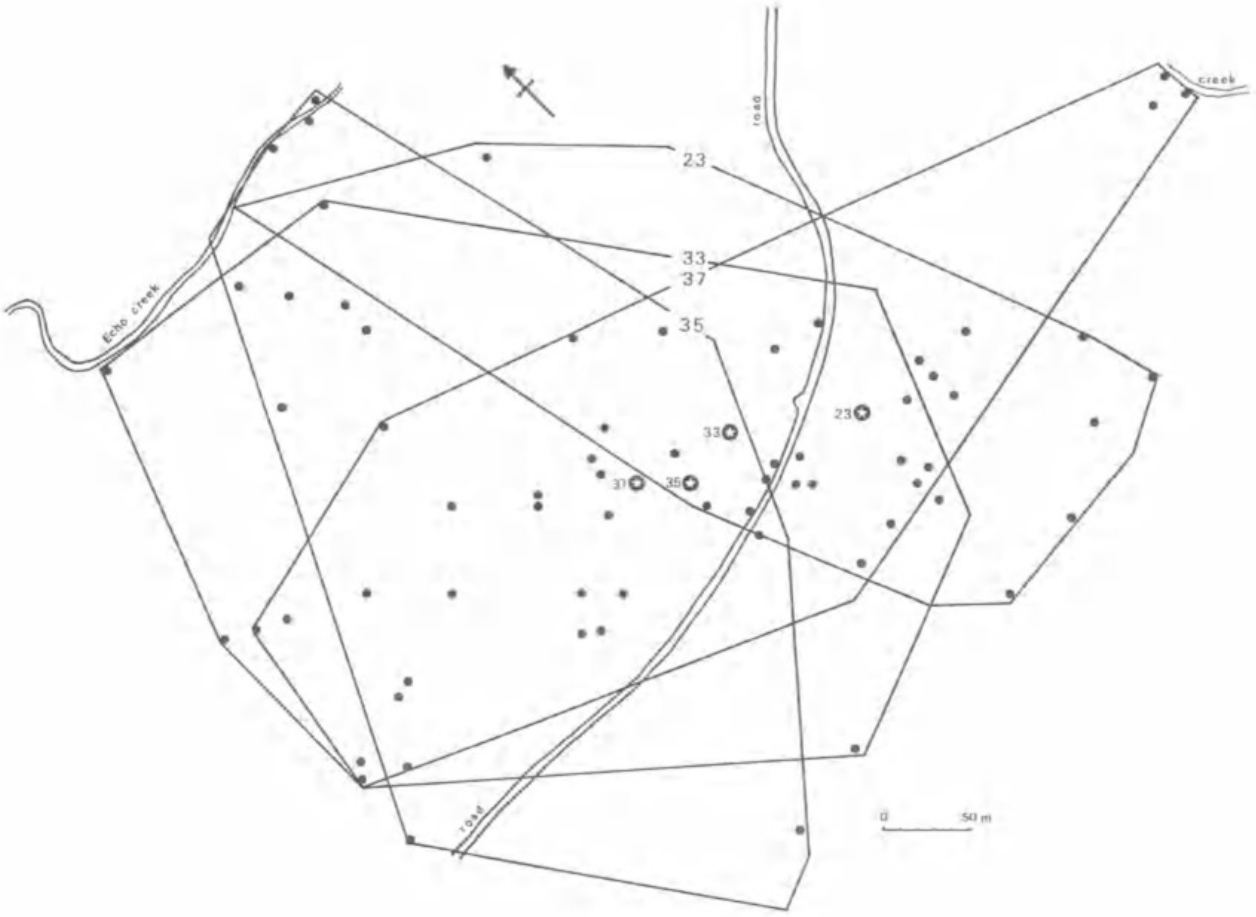

FIG. 1. Minimum Convex Polygon home range areas (n = 636 fixes*) for four male Tooth-billed Bowerbirds, based upon their adjacent courts, during the 1989 display season. Numbered stars = male's court location and number. Solid dots = sightings of males in tree canopy.* male 23 = 202 fixes; 33 = 148 fixes; 35 = 122 fixes; 37 = 164.

the bird. This problem increased the further the male travelled from his court. In addition, male Tooth-bills are well camouflaged and rely on cryptic habits to avoid predation (Frith & Frith, 1993, 1994). For these reasons it was often difficult and sometimes impossible to establish either the final destination or the activities of a bird, leaving the reason for many forays by a bird as unknown, and destinations as approximate areas only.

In this paper absences from courts are classed broadly as foraging, non-foraging and unknown activities. Foraging absences were those primarily concerned with visits to food trees where fruits were eaten but sometimes brief non-foraging activities were observed before or after feeding. Non-foraging absences did not include visits to fruiting trees or, the the best of our knowledge, feeding. Foraging and non-foraging activities were either observed directly or inferred from characteristics of the destination of the bird, the radio signal or sounds from the canopy. Direct return flights from a destination tree to a court were determined by the rapid loss of a signal and the subsequent recording of the male at the court by DWF in the hide.

Many home range estimators are available for home range analysis (Mohr, 1947; Southwood, 1978; Anderson, 1982; Worton, 1989). Following animals using focal sampling results in autocorrelation of locations (i.e. non-independent fixes). This may create problems in the analysis of radio-tracking data. However, several recent studies have found that home range estimates based on independent versus non-independent locations are statistically indistinguishable (Anderson & Rongstad, 1989; Gese et al., 1990). As most fixes obtained during this study were

TABLE 1. Three-way fixed factor Analysis of Variance * examining the effect of month, time period and individual male on home range estemates for four male Tooth-billed Bowerbirds during peak activity of the 1989 display season.

Treatment	df	F	P
Month	2	1.43	0.269
Time period	3	1.26	0.320
Individual male	3	2.31	0.115
Month x Time period	6	0.22	0.965
Time period x Month	9	0.36	0.938
Month x Time period x Bird	16		
Total	39		

* = values obtained using Minimum Convex Polygon method

non-random the Minimum Convex Polygon (Mohr, 1947; Southwood, 1978) estimator was used to estimate home range size. This method is sufficiently robust to deal with non-independence of locations. Home range and home range overlap were estimated using the commercial package Ranges IV.

Most frequency distributions of time and space use about a court by the male owner were highly skewed towards the court; therefore the median was chosen as the best indicator of the central place tendency of the data, rather than mean (Zar, 1979).

RESULTS

Home Range

The mean home range area for four male Tooth-bills over the 1989 display season was 9.5ha (range 6.9-12.5) as determined from a total of 636 fixes obtained away from courts (Fig. 1). In a three way fixed factor analysis of variance examining the effect of month, daytime period and individual on the home range estimate, there were no significant differences (Table 1). Mean overlap of the four home ranges was 50% with a range from 23-80% (Fig. 1, Table 2). There was a significant difference in the amount of overlap observed between individual males and their nearest neighbours (one way Analysis of Variance using arcsin square root transformed proportions: $F = 6.36$, $df = 3$, $P = 0.0164$). The greatest home range overlap was observed between males whose courts were closest together (Fig. 1, Table 2).

The median distance males travelled from their courts for all activities was 59m, with a minimum of 8m and maximum of 391m (Table 3). Minimum distances occurred when males stole leaf decorations from a neighbour's court or chased off conspecifics a short distance from their own court. Maximum distances occurred when males flew to a creek to bathe, usually in the middle of the day. The nearest significant body of water was located in a gully about 300m from the courts (Fig. 1).

TABLE 2. Percent overlap of the home ranges of four radio-tagged male Tooth-billed Bowerbirds away from their courts during peak activity of the 1989 display season.

Male	23	33	35	37
23	-	55.0	32.4	45.1
33	30.7	-	64.8	54.7
35	22.6	79.6	-	47.7
37	36.6	76.6	56.2	-

Time Utilisation

Males spent an average of 64% (range 56-73%) of total time (0600-1800h) attending courts during peak activity of the 1989 display season. Up to 3% of this time present males were detected above their courts by radio signals, but remained unseen or unheard by the observer in the court hide (see Frith & Frith 1994: table 3). In a three way fixed factor analysis of variance examining the effects of month, daytime period and individual male on the proportion of time spent at the court during 1989, there were no significant differences (Table 4). Court attendance levels and time-budgeted activities at courts by the four males during different months (October-December) and during different times (0600-1800h) of the day during this season are reported elsewhere (Frith & Frith, 1994). The results of radio-tracking at courts at night revealed that each male Tooth-bill roosted above his court.

Males spent an average of 36% (range 27-44%) of total time (0600-1800h) absent from their courts during peak activity of the 1989 display season, with a mean duration per absence of

TABLE 3. Distances (m) of all movements away from courts by four male Tooth-billed Bowerbirds during peak activity of the 1989 display season.

Male	Number of fixes	Median distance	Minimum distance	Maximum distance
23	202	50.6	27.2	384.8
33	148	58.6	13.9	370.7
35	122	86.4	14.3	311.3
37	164	40.4	8.2	391.4
Total	636	59.4	8.2	391.4

TABLE 4. Three-way fixed factor Analysis of Variance * examining the effect of month, time period and individual male on proportion of time four male Tooth-billed Bowerbirds spent at their courts during peak activity of the 1989 display season.

Treatment	df	F	P
Month	2	0.51	0.6091
Time period	3	0.12	0.9494
Individual male	3	1.06	0.3918
Month x Time period	6	0.21	0.9700
Time period x Month	9	0.21	0.9885
Month x Time period x Bird	16		
Total	39		

* = using arcsin square root transformed proportion data.

13.1mins (range 8.4-17.7). The proportion of total time males were absent and the mean duration of absences were lower during November than during October or December. Males spent less time at courts during the middle of the day between 0900-1500h (Table 5).

During the first hour (0600-0700h) of the first October tracking period male 33 cleared a small subsidiary court some 40m away from his primary one. Because this unusual behaviour may have been caused by banding, transmitter attachment or both the records from this hour have been excluded from analyses. During subsequent October tracking periods this male occasionally flew over, and perched briefly above, the rudimentary court (<3% of total time absent from his established court). Male 33 spent more time absent from his court than the other three males and Male 37 spent less time absent (Table 5), but differences between the four males were not significant ($\chi^2 = 3.78$, $P > 0.02$).

Activities Away From Courts

Of 197 total absences from courts 119 were foraging absences (60%), 35 non-foraging absences (18%) and 43 absences with unknown activities (22%), representing 82.8, 6.8 and 10.4% of total time absent respectively (Table 5). A foraging absence averaged 17.9mins (range 11.4-24), a non-foraging absence averaged 5mins (range 2.9-13) and an absence with unknown activities 6.3mins (range 5.1-6.9, Table 5).

During foraging absences the birds were seen in destination food trees for 67% of the time; the remaining time being spent en route to or from the court (30%) or performing non-foraging activities (3%). Sixty six of the 119 foraging absences were to known food trees. The median foraging distances travelled by three males to these trees ranged from 19-42m, but male 37 flew much further to forage, with a median distance of 119m.

During a foraging absence males usually flew directly from the court to a food tree. On eight occasions, however, a court-owning male chased a conspecific from his court before continuing on to a food tree (see below). Males also occasionally flew directly towards a creek (before or after feeding) where it was assumed they went to bathe or drink, but trackers were only able to visually confirm this twice. Most times (86% of foraging absences) the bird flew directly back to the court

TABLE 5. Activities performed by four individual male Tooth-billed Bowerbirds during absences from their courts over peak activity of display season.

ABSENCES:		FORAGING			NON-FORAGING			UNKNOWN ACTIVITIES			TOTAL		
Male	Hours of radio-tracking	Number of absences	% of time absent	Mean mins @ absence	Number of absences	% of time absent	Mean mins @ absence	Number of absences	% of time absent	Mean mins @ absence	Number of absences	% of total time absent	Mean mins @ absence
Male													
23	36	43	84.6	16.1	5	7.9	13.0	12	7.5	5.1	60	13.6	37.9
33	23	26	90.8	21.2	5	3.7	4.6	5	5.5	6.8	36	16.9	44.1
35	24	21	89.8	24.0	7	6.2	5.1	4	4.0	5.6	32	17.7	39.2
37	36	29	65.3	13.1	18	8.6	2.9	22	25.9	6.9	69	8.4	27.0
Month													
October	47	39	80.6	19.9	15	8.9	4.7	16	10.6	6.8	72	13.4	34.1
November	36	35	78.4	13.9	13	9.0	4.2	16	12.6	4.9	64	9.7	28.6
December	36	45	87.5	18.3	4	3.5	6.8	12	9.0	7.6	61	16.3	46.0
Time													
0600-0900	29	32	76.5	11.4	16	10.3	3.1	10	13.2	6.3	58	8.2	27.4
0900-1200	30	28	85.1	22.0	4	3.4	6.1	13	11.5	6.4	45	18.1	40.1
1200-1500	30	29	80.1	20.9	6	8.3	10.5	15	11.3	5.7	50	15.1	41.9
1500-1800	30	30	77.8	18.2	9	6.2	4.3	5	6.1	7.6	44	14.1	34.5
Total/means/%	**119**	**119**	**82.8**	**17.9**	**35**	**6.8**	**5.0**	**43**	**10.4**	**6.3**	**197**	**13.1**	**36.0**

but on 15 occasions (14% of foraging absences) a leaf decoration was collected during the return trip. It is possible that undetected activities occurred during flights between courts and food trees.

Of the 35 non-foraging absences 12 entailed collection of a leaf decoration from a tree (3 leaves) or from another court (9 leaves), 12 were visits to the forest canopy above a neighbouring courts, and 11 involved the male court-owner chasing a conspecific and then returning immediately to his own court (see below). Theft involved a male flying directly to a neighbouring court, quickly and quietly stealing a leaf from it, and returning directly to his own court. Leaf theft represented 0.5% of total time absent from the court, with a mean duration of 1.5mins per theft. The 12 visits to a neighbouring court were brief and involved the court-owner flying directly to, and perching quietly above, his neighbour's court for a short period (mean duration = 3.3mins), possibly with the intention of stealing a leaf. This behaviour was performed by all four males.

Males were seen to chase conspecifics away from the court on 19 occasions flying on to a food tree after eight such chases and returning directly back to the court after 11 of them. Three chases were in pursuit of a presumed female (having previously been displayed to). It is possible other chases were after a neighbouring male. On one occasion a leaf was stolen by a marked, neighbouring male just as Male 37 returned to his court. The latter male immediately chased the thief to the thief's court, about 70m away, where he stayed briefly before returning to his own court without a leaf. He was, however, subsequently seen to steal from that particular neighbour's court.

Interactions between conspecifics were observed away from the court. On four occasions a male left his court and flew to where other Tooth-bills were heard displaying, either above or on another a court. On one occasion Male 35 was seen calling and displaying to an assumed female near a creek that was about 300m from his court. On two occasions two birds were seen facing each other in a food tree, face to face, with conspicously sleeked plumage and agitated vocalisations.

DISCUSSION

Beehler & Pruett-Jones (1983) reviewed available information concerning the spatial dispersion of adult males of nine polygynous bird of paradise species (Paradisaesidae) from New Guinea rainforests. These species were known or presumed to involve promiscuous males. Males of species with a predominantly arthropod diet were found to be territorial while males of predominant frugivorous species were non-territorial. Lack of territoriality in predominantly frugivorous passerine species is considered to result from the fact that tropical fruits are economically undefendable (Lill, 1976; Beehler, 1989; Beehler & Pruett-Jones, 1983).

During the 1989 display season the mean home range size of male Tooth-bills was 9.5ha and the median distance travelled from courts for all activities was 59m. Comparable data on the breeding season home range of other tropical frugivorous birds which display at focal sites are scarce. Pruett-Jones & Pruett-Jones (1988) reported that the home range of one adult male Blue Bird of Paradise, *Paradisaea rudolphi*, was 4.7ha over the season, about half the size observed in male Tooth-bills. Display trees of the former species are much more widely spaced than are the courts of Tooth-bills (220m vs 50m respectively). Blue Birds of Paradise are not as exclusively frugivorous through the breeding season as are Tooth-bills (cf. Beehler & Pruett-Jones, 1983) and this, together with a possible greater abundance of food near display sites, may account for differences in home range sizes between these similar sized species. It is noteworthy that the all-purpose territory of three male Superb Birds of Paradise, *Lophorina superba*, a species with only 24% fruit in its diet, averaged 1.5ha (range 1.2-1.7) (Beehler & Pruett-Jones, 1983). The availability of fruit in time and space may therefore have major effects on both male dispersion and home range.

Male Tooth-bills do not move far from their courts and, as would be expected, males at an exploded lek exhibit considerable overlap (mean = 50%) of home ranges. Those with closer courts show the greatest overlap, and males from different courts were observed to bathe in the same portions of creeks and to feed in the same trees. Although distances incurred in travelling to bathing and drinking locations, or those associated with leaf thefts, are likely to remain constant across years this will not be true of distances travelled to and from feeding locations. These latter distances will vary between years as different individual trees or species of tree fruit. Seasonal environmental differences, in particular fruit crop size, affect the length of Tooth-bill display seasons and the proportion of time that males attend courts (Moore, 1991; Frith & Frith,

1994). Fruit crop was poor during the 1989 display season (Moore, 1991). Consequently, males spent a greater proportion (36%) of their time absent from courts, to feed, during the 1989 season than during the 1980 season (21%) when fruit was abundant (Frith & Frith, 1994). During the exceptionally dry 1979 season an extremely poor fruit crop resulted in males spending even more time (48%) away from courts (Frith & Frith, 1994).

All the observed movements away from courts appeared to entail direct purposeful flights to food, water or leaf (court decoration) resources. Activities such as interactions with conspecifics or the collection of leaf decorations that were observed away from courts, during both foraging and non-foraging absences, were extremely brief (Table 5). Most absences were for foraging, representing 83% of total time absent with a mean duration of 18 mins (Table 5). Moore (1991) found that Tooth-bills tended to forage more in food trees closer to the court than those further away and as a result shorter foraging absences were more frequent than longer ones. Median distance travelled from courts exclusively for foraging at food trees was 32m (median range 27-119). Male 37 flew much further than the other three males to forage, often visiting fruiting trees some 380m to the east of his court that were not visited by the other males studied (Fig. 1). While males other than those of this study doubtless fed in these trees the observation suggests the possibility that males on an exploded lek may travel greater distances to utilise rich food resources where competition may be less. It is possible, however, that Male 37 also fed in this area due to the local accessibility of the creek (see Fig.1).

Donaghey (1981) presented the only comparable data. He found that five rainforest-dwelling male Satin Bowerbirds, *Ptilonorhynchus violaceus*, mostly foraged for food within 50m of their bowers (83% of 83 foraging records) during the breeding season of October-December. He obtained almost identical results for four woodland-dwelling males (82% of 273 foraging records within 50m of bowers). His Satin Bowerbird's bowers did not form leks but were dispersed linearly along forest edges at a mean inter-bower distance of 312m (Donaghey,1981).

Male Tooth-bills, like male Satin and other bowerbirds, must remain close to their court if they are to successfully display and attract females to mate (Frith & Frith, 1993) as do males of other, mostly lekking, passerines (Snow, 1962; Lill 1974a, b). Thus, irrespective of the size of a meal eaten or the distance travelled to the food, males almost invariably return directly to their court in order to defend it from leaf stealing rivals and to call and display. In effect, male Tooth-bills attempt to maximise their time at their court (Moore, 1991). They can achieve this, however, only by utilising a food resource that is freely available and unable to be defended, namely, fleshy fruits. Snow (1976) considered a predominantly frugivorous diet one of the main pre-conditions to a mating system lacking pair bond and biparental brood care in which males spend much time attending and defending a traditional courtship area.

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