The acoustic communication of the Polynesian megapode *Megapodius pritchardii* G. R. Gray*

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The acoustic communication of the Polynesian megapode *Megapodius pritchardii* G.R. Gray, 1864, was studied and analysed for the first time. Adults pair up monogamously and the male produces so called whistles while guarding its mate. The three-element song of the male together with the females`s "coo" call are combined to produce a duet. Depending on the social context, either sex may initiate the duet. Both male song and duet serve mainly in territorial defence. Neighbouring pairs often answer by producing the same sound in response to any one of three vocalizations (song, duet, whistle). "Clucks" are additional sounds with a social function uttered by both sexes. When handled, adults and chicks utter "distress calls"; in chicks, these are the only sounds recorded. Other *Megapodius* species seem to have a similar sound-repertoire as the Polynesian megapode.

Introduction

Megapodes are fascinating birds, especially because they leave the incubation of the eggs to external heat sources and do not care for the young. Accordingly, many publications deal with breeding strategies of these birds (e.g., Diamond, 1983; Jones & Birks, 1992; Jones et al., 1995), whereas their habits away from the breeding sites and especially the acoustic communication have not been investigated in much detail (Jones et al., 1995).

Most megapodes live in dense rainforests and behave secretly. Sounds are the best tool to communicate under such circumstances. Often sound seems to be used for supplementing territorial behaviour or defence. The Australian brush-turkey *Alectura lathami* J. E. Gray, 1831, for example, utters a deep boom to drive off others from the mound (Jones & Birks, 1992). Territorial behaviour includes duets in some megapodes, and these may also serve pair bonding (malleefowl *Leipoa ocellata* Gould, 1840, Immelmann & Böhner, 1984; orange-footed megapode *Megapodius reinwardt* Dumont, 1823, Crome & Brown, 1979). Duets may, in certain situations, be an indication of monogamy (Farabaugh, 1982).

In this paper, we present all known vocalizations of the Polynesian megapode *Megapodius pritchardii* G. R. Gray, 1864, and give explanations for their function, as obtained from the behavioural context. The Polynesian megapode, locally called Malau, lives endemic in dense forests on the island of Niuafo'ou in the Kingdom of Tonga, Polynesia. It lays eggs year-round and buries them in volcanically heated soil

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(laying burrows, Göth & Vogel, 1997). Todd (1983) investigated egg laying activities and made preliminary observations of its behaviour and voice. Rinke (1986, 1993) described some calls of the birds. The study on vocalizations presented here is the first for any of the 13 species of the genus *Megapodius* Gaimard, 1823. It could also be of relevance for megapodes of the other six genera, for which little is known about (the function of) their voices (Jones et al., 1995).

Methods

The island of Niuafo'ou is a collapsed volcano, 8 km in diameter, with a crater lake containing three islets. The habitat of the Polynesian megapode, dense forest rich in understorey, is mainly found on the inner slopes of the caldera and on the islets in the crater lake (for maps of Niuafo'ou see Göth & Vogel, 1995, 1997).

This study took place on the islet of Motu Molemole (MMM, 12 ha) in the crater lake from October 1991 to January 1993, with five breaks of 2-3 weeks each. From October 1991 to January 1992 we (Göth & Vogel) visited MMM sporadically, thereafter we stayed in an island camp daily, except for sundays. Altogether there have been about 1300 hours of field work on 232 days. MMM was chosen because the density of the megapodes was rather high with 1-1.2 pairs per ha (Göth & Vogel, 1995). An agreement with the inhabitants of Niuafo'ou safeguarded MMM against undesirable intrusions during the study, so undisturbed working was generally possible.

Polynesian megapodes were caught in self-made walk-in traps (bottom area 2 × 3 m, height 1 m) covered with nets. The traps were spread over 13 different sites on MMM for 1-2 week periods and checked every three hours. Megapodes were never caught near the laying-burrows, since females with an advanced egg tend to incur injuries (Dekker, 1990). Altogether 20 of the 24-28 adult Polynesian megapodes living on MMM were caught. They were measured, marked with coloured leg-rings and released where they had been caught.

Sex determination based on plumage characters was not possible. Only once a male and female were caught together and the male could be identified by its more orange legs. Additional information on sex was sometimes gained by the large weight of the female carrying an egg (Göth, 1995). However, sex determination was possible afterwards when the behaviour of the megapodes was being observed, for instance when ringed females laid an egg or paired ringed males defended their territory.

Two of the three laying burrows on MMM were monitored from a hide at a distance of 4 m for at least two hours daily. For observations away from the burrows daily patrols of at least 2h were undertaken, thus monitoring all parts of MMM. Behaviour and vocalizations were recorded in relation to time of day and weather. Due to the small number of megapodes studied (maximum 28 individuals) the same birds were observed repeatedly, so the data are not independent.

After some weeks we could safely assign the sounds to the sexes and to one of several sound types. The accompanying behaviour as well as the number and, if possible, identity of the calling megapodes were recorded. Which part of the duet (see below) was produced by which sex could be determined reliably only after about three months, when pairs had been seen duetting several times at close range.

Sounds were recorded with a Sony Walkman WM-D3 and a Sennheiser microphone MKH 805. Sonagrams were analysed with the sound-analysing program AVISOFT (R. Specht, Berlin, 1992) with the following settings: N 256, Hamming window N/2, step N/2, threshold frequency 8 kHz. To collect as many high quality recordings as possible, Polynesian megapodes were stimulated into responding vocally by playback of songs and/or duets. In these experiments the vocalizations of individuals from outside MMM were played back with natural loudness from a separate loudspeaker, placed in a tree about 3 m above the ground and 4 m away from the observer. A song or duet was always played back four times at intervals of 5 min. during which all behavioural actions were noted. To us, the sounds of the birds responding to playback did not differ from naturally occurring sounds.

It is presumed that Polynesian megapodes are monogamous (Vogel, 1995). Therefore, a pair is considered as two individuals which stay close together most of the time and are never seen with another partner, except for short agonistic interactions.

Results

Whistles

Whistles are the sounds most frequently heard from both male and female. The single whistles, recognisable as 2-3 bands in the sonagram (fig. 1), follow each other in bouts of 3-5 whistles that may be rendered phonetically as "tit-tit-tit...". Whistles in a bout have about the same pitch (table 1), but get softer towards the end.

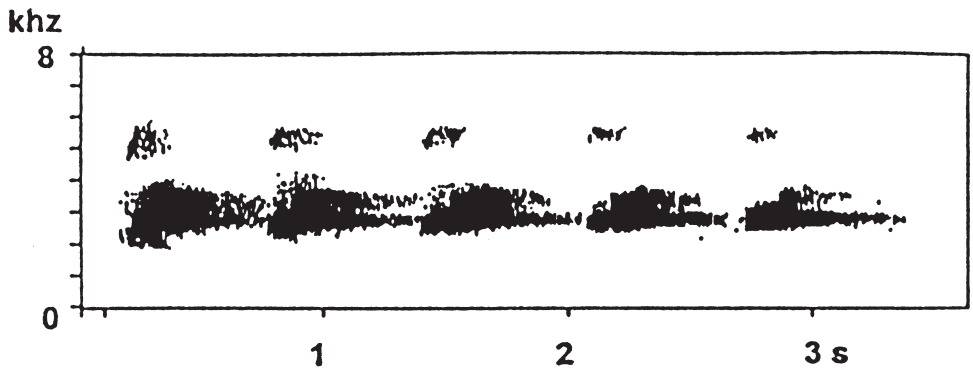

Fig. 1. Bouts of whistles of a male Polynesian megapode *Megapodius pritchardii* G. R. Gray, 1864, during disturbance.

Bouts of whistles were uttered, for instance, when a barn owl *Tyto alba* (Scopoli, 1769) flew over a pair, or during fights. Most commonly, the megapodes whistled while fleeing from the observer. Whenever a pair was disturbed, one partner (almost always the male) whistled briefly and both male and female fled in different directions. If a megapode discovered one of us from a distance, it whistled in longer bouts, shortly after followed by its mate; both birds then ran away in the same direction. In a third type of encounter, when the observer was hidden and not visible to the megapodes, the male alone whistled briefly as it approached, presumably to investi-

Table 1. Parameters of different vocalizations of the Polynesian megapode obtained by sonagraphic analyses with the computer program AVISOFT. All values given as mean ± S.D., E1-E3 = Elements 1-3 of song.

Vocalization	from	Duration (s)	Center of frequency (kHz)	Sample size	Context
Whistle	male female	0.4 ± 0.05	2.7 ± 0.1 (band 1) 3.4 ± 0.2 (band 2) 5.3 ± 0.1 (band 3)	8 bouts of whistles	alarm call (mate guarding)
Cluck	male female	very short	?	-	when fleeing, in combination with whistles
Distress call	male female	0.3 ± 0.2 (adult)	1.2 ± 0.1 (adult)	4 adults	when held in hand
	chick	0.4 ± 0.1 (chick)	1.9 ± 0.1 (chick)	2 chicks	
Song	male	0.6 ± 0.1 (E1) 0.3 ± 0.1 (pause) 0.5 ± 0.1 (E2) 0.9 ± 0.1 (pause) 1.0 ± 0.1 (E3)	2.0 ± 0.2 (E1) 3.0 ± 0.2 (E2) 2.1 ± 0.1 (E3)	19 songs of 19 different males	territorial defence, pair bonding, part of duet
Coo	female	1.2 ± 0.1	1.4 ± 0.03	5 coos	during territorial fights, playback and interactions at the laying burrow, part of duet
Duet	male & female	see song and coo	see song and coo	-	mainly territorial defence, pair bonding

gate the minor disturbance. As soon as the megapode discovered the human intruder, it whistled in long bouts. The hen sometimes "coo"-ed (see below) simultaneously with the males whistles and both then disappeared in the same direction. The male whistled prior to the female on 30 of the 32 observations made of fleeing pairs (for all three types of encounters with the observer described above). At the laying burrows, the male which occupied a territory in which a burrow was located always whistled when expelling a strange female visiting the burrow. While the female was being pursued by the territorial male, she also whistled.

"Distress call"

Males and females, which upon capture were being held by their legs, uttered croaking calls in bouts. Beside the basic frequency, three to four overtones can be recognised in the sonagram (fig. 2). Since Polynesian megapodes utter these calls exclusively in a threatening situation, we call them "distress calls". Usually a few "distress calls" are uttered in bouts for periods up to 30-60 s.

Sounds of the chick

When held in the hand, two out of six chicks uttered calls similar to the "distress

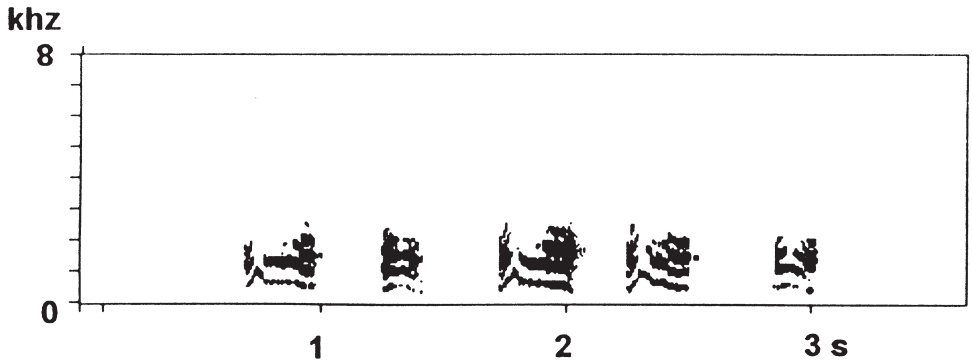

Fig. 2. "Distress-calls" of an adult female Polynesian megapode *Megapodius pritchardii* G. R. Gray, 1864, held in the hand.

calls" of the adults. They are also composed of a basic frequency and one or more overtones, but the distance between the frequency bands is wider. As in the adults, the "distress calls" were uttered in bouts spread over up to one minute. Fig. 3 shows part of such a bout of a chick at the age of five or six days. The frequency and time structure of this call did not change till the end of recording on the 51st day of age of the two chicks in question. In the aviary, the six chicks never uttered any calls.

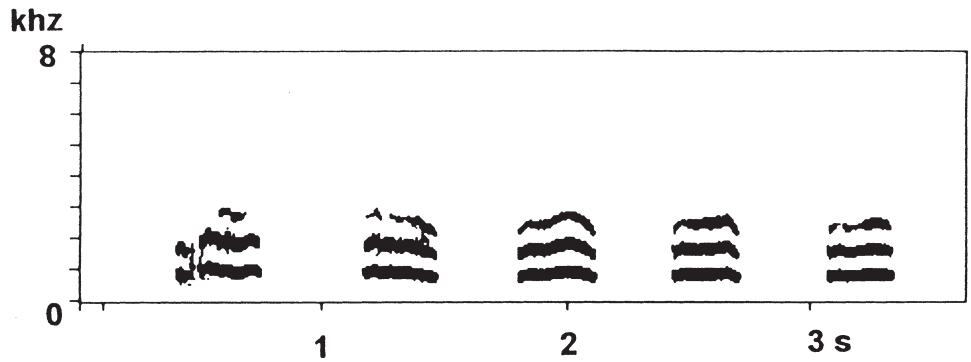

Fig. 3. "Distress calls" of a chick Polynesian megapode *Megapodius pritchardii* G. R. Gray, 1864, held in the hand at its fifth or sixth day of life.

Cluck

The cluck vocalization consists of a single element with a duration of only a few tenths of a second. It can only be heard at close range and is uttered by both male and female. We were unable to obtain sonagrams of this sound. Since they are very soft, clucks were not heard often. When disturbed, megapodes which seemed out of reach of their partner sometimes clucked while fleeing. In one instance, a female that was scratching in a laying burrow responded with clucks to whistles of her approaching male. The male then stopped whistling and started clucking, whereupon the pair left the burrow. Similarly some females also uttered clucks upon ending their bouts of whistles, or they clucked inbetween single whistles.

Song of the male

A song is characterised as a strophe, produced by the male and composed of three elements (E1-E3, fig. 4). Phonetically it can be rendered as "deee-ded-drrrr". While singing, the male stands in a hunched posture.

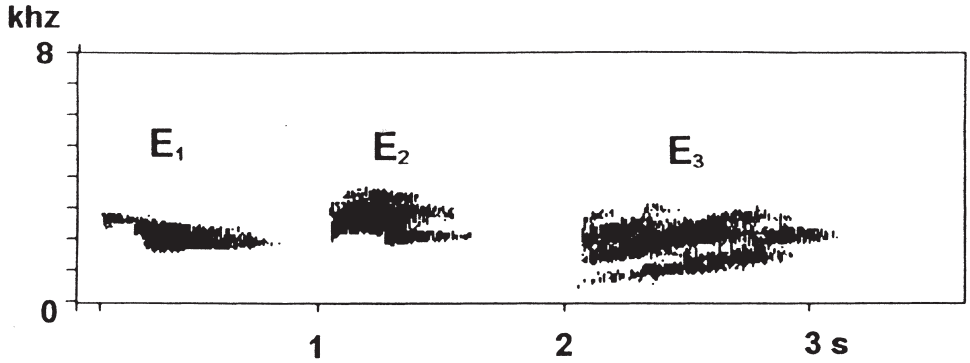

Fig. 4. Song of a male Polynesian megapode *Megapodius pritchardii* G. R. Gray, 1864, (E1-E3 = song elements).

The elements E1 and E2 remain at about the same pitch. E2 is the loudest element of the song. The frequency of the last element E3 first rises and then falls (about 20 times/s) and hence sounds like a warble. The main part of E3 is a small band of unchanging pitch with two weaker side bands of changing pitch above and below it.

The song elements of individual males are very similar in duration and frequency (table 1). Invariably the strophe is given as a full song. Inter-individual differences exist in the frequency modulation of the single elements, especially in E3 the form of the upper and lower frequency band varies. In E2 the two frequency bands can be separated or fused to one wide band. Therefore the song of different males can sometimes be discriminated quite easily, which was helpful for acoustic identification of individual males.

The song presents the males part in the duet and its behavioural context is described below. In isolation, it occurs either when the male is unpaired or the female does not join in to produce a duet.

"Coo" of the female

The "coo" is a quavering sound, similar in structure to the last element E3 of the male song, but lying 0.7 kHz lower (table 1, fig. 5) and being softer. In the forest, one cannot hear it from more than 50 m distance. It did not differ between individual females.

The "coo" is heard most frequently as the female's part in the duet (fig. 5). Sometimes the female "coo"-es while the male whistles (fig. 6). In isolation, the "coo" is uttered during territorial fights and playback trials (see below). Additionally, "coo's" occurred during interactions at two laying burrows on MMM, which were only big enough for one female at a time. During three observations, when two females met at the burrow to lay an egg, they chased each other a few times and "coo"-ed. The loser returned later and began to "coo" some distance from the burrow. As soon as the dominant female noticed her she again chased her away.

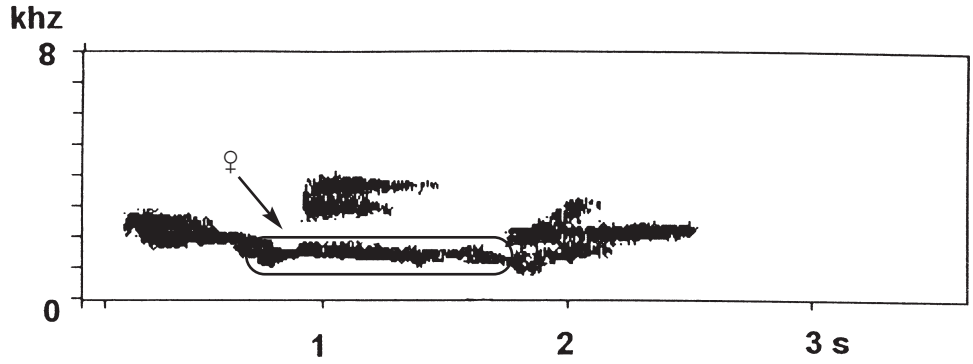

Fig. 5. Duet of the Polynesian megapode *Megapodius pritchardii* G. R. Gray, 1864, in its "normal form", in which the male starts. The encircled element is the females` part ("coo"), all other elements being from the male song (see Fig. 4).

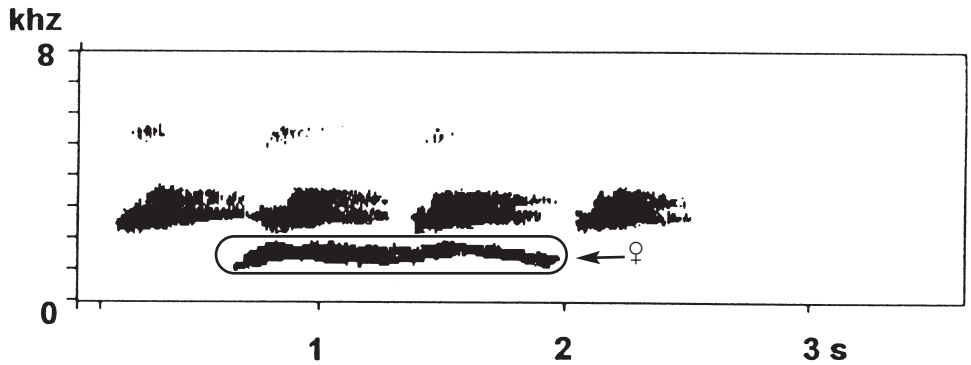

Fig. 6. Bouts of whistles of a male and coo of the female Polynesian megapode *Megapodius pritchardii* G. R. Gray, 1864, during disturbance.

Duet

In a duet, one individual generally coordinates its sound in time and sometimes in structure with that of its partner (Wickler, 1974). In the duet of the Polynesian megapode, male and female produce different sounds, and generally one partner joins in before the other has finished its part. Typically (see below), the male initiates a duet with his song. The "coo" of the female can then follow at any time between the beginning of the first and third element of the male song, and it always ends before the male has finished his complete song. This we regard as the "normal form" of the duet (fig. 5). A second form occurs when the female starts the duet: she "coos" and the male answers immediately after the onset of her "coo" with his complete song (fig. 7). The duet is not accompanied by any conspicuous movements, as in other birds (Seibt & Wickler, 1977). The male assumes his hunched song posture; the female has her neck slightly drawn in, as when resting.

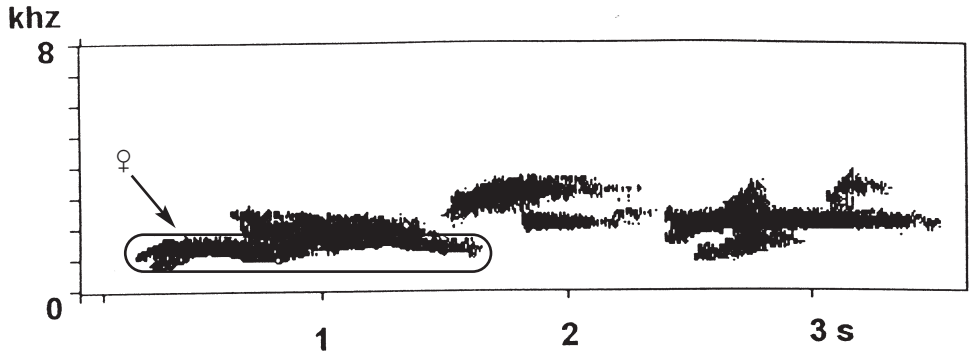

Fig. 7. Duet initiated by the female Polynesian megapode *Megapodius pritchardii* G. R. Gray, 1864.

Behavioural context of song and duet

Since both vocalizations occur in similar situations, they are dealt with here together. Quite often song and duet seem to be provoked by environmental noises like the calls of doves (*Ducula pacifica* Gmelin, 1789, *Ptilinopus porphyraceus* Temminck, 1821), (walking) noises of goats or humans, or thunder. Mostly, however, song and duet are uttered during territorial defence and when mounting trees to spend the night.

Songs and duets during territorial defence

From January 1992 to January 1993 more than 250 observations of marked megapodes were made on MMM. Only once a bird was seen more than 100 m away from where it had been caught or seen for the first time (observations of females at the laying burrow are not included since there was often no burrow in their own territory). Hence, it is assumed that Polynesian megapodes hold and defend territories.

Polynesian megapodes sing or duet at all times of the day and year. Usually there is one song or duet followed by a pause of at least five minutes (in 60 % of 93 cases), a few times there was a bout of vocalising (2-22 times). Songs occur more often than duets. For example, during a day on which one pair was monitored from 6.00 to 8.30h and from 10.00 to 18.30h, 21 songs of the male were heard, but only four duets.

Songs, duets and whistles were often answered within a few seconds by neighbouring males or pairs. Such provoked calls between holders of neighbouring territories which are coordinated in time are here called "counter calls" if less than 1 minute elapsed between call and response. Often the neighbours answered with the same type of vocalization in counter calls, hence there seems to be some kind of "signal matching" during vocal interaction between pairs (fig. 8). Altogether, duets were answered more frequently than songs or whistles.

During counter calling the megapodes were usually moving on the forest floor searching for food. During 21 patrol walks (each lasting 2 hours) a total of 15 episodes of counter calls were heard. These episodes differed readily from other ones that occurred before and after a fight between two territorial neighbours (three observations during the 21 walks). A fight was preceded by a more frequent "counter-duetting" or "counter-singing" than usual. Whenever a male or pair intruded the neigh-

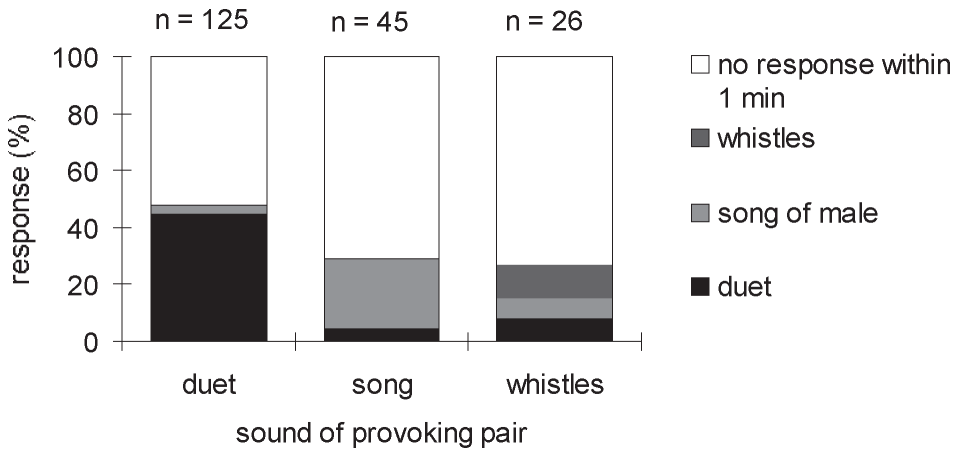

Fig. 8. Relative frequency of vocalizations, which were used by territorial pairs of the Polynesian megapode *Megapodius pritchardii* G. R. Gray, 1864, while answering different types of vocalizations within one minute during seven series of "counter calls" (duration 30-98 min, median 44 min) with 276 vocalizations (11 pairs, 2 tested twice). More than one response to one call was counted as only one.

bouring territory, the territorial male immediately flew towards the intruder(s) and whistled. A silent fight mostly ensued between the two males, while the females regularly "coo"-ed from nearby. At some point, the loser ran or flew away while uttering whistles, followed by the winner. In all three such observations the winner was the male holding the territory. Following the dispute, the winner duetted with his mate for several minutes. The expelled birds responded with duets after having returned to their own territory. The increased singing and duetting ceased again after 5-20 min.

During playback, when songs or duets of other Polynesian megapodes (i. e. from outside MMM) were played, the territorial male always (n = 51) flew towards the speaker within a minute. He landed in a nearby tree with his neck extended while whistling. The female always approached a few minutes later, walking why she was "coo"-ing or duetting with her partner.

Songs and duets during roosting

At night Polynesian megapodes roost in trees which they mount at dusk and descend again early in the morning. Males and females seem to choose different trees; whenever we were able to observe both partners (five times), they ascended 5-30 m apart. As they slowly climb and flutter from branch to branch, all pairs duet. On average, a pair duets four times (median) per evening (range 1 - 15 times; n = 112 duets of 23 pairs on 9 evenings) for a period of 10 min. (median) (range 1-19 min.; n = 23 pairs on 9 evenings).

During the night pairs duet irregularly every few hours from the trees, mostly 2-3 times in a row. Often a few pairs duet or single males sing simultaneously. However, playback of songs or duets during the ascent or the night provoked no answer. In the morning, shortly after descending the tree, the partners duet a few times in a row. Whether the mated birds have reunited at this time could not be determined.

Who initiates the duet - female or male?

Fig. 9 shows that males and females differ significantly in the frequency with which they initiate the duet under different situations ($Chi^2 \leq = 77.17$, d = 3, p= 0.001). These situations were as follows:

(1) During our *patrols*, the "normal form" of the duet (initiated by the male) was most frequently heard.

(2) After a *fight* between territorial pairs females rarely started a duet.

(3) During *mounting a tree for roosting*, the hens were the initiator more frequently than in (1) or (2).

(4) During *playback*, the females initiated the duet more frequently than the males.

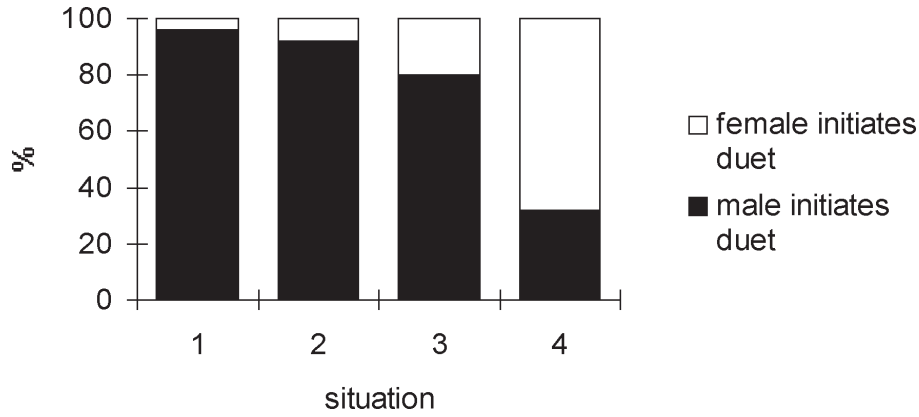

Fig. 9. Proportion with which one of the partners of a pair of the Polynesian megapode *Megapodius pritchardii* G. R. Gray, 1864, initiated the duet in four different situations: 1 = during the patrol walks (n = 68 duets during 28 h of observation), 2 = after a fight (n = 152 duets after 6 fights), 3 = during ascent to roost (n = 112 duets during 9 evenings), 4 = after playback (n = 31 duets after 8 playbacks). The following number of pairs was represented in the single situations (in brackets number of birds represented more than once): 1: 13 (2 2 ×; 2 3 ×); 2: 10 (1 2 ×, 1 3 ×); 3: 11 (5 2 ×, 1 3 ×); 4: 9.

Discussion

Signal function

For Polynesian megapodes, inhabitants of woods rich in understorey, sounds should be a more effective way of communication than visual signals (Diamond & Terborgh, 1968). Duets and songs, especially, carry far; when the weather is calm the megapodes seem to hear each other over a distance of more than 100 m, answering each other within 30 seconds.

Songs and duets in birds can serve the announcement, formation and strengthening of the pair-bond and may be seen as indicators of monogamy (Thielcke, 1970; Thorpe, 1972; Farabaugh, 1982). Duets of tropical birds commonly coincide with a long-lasting pair bond (Kunkel, 1974). They may synchronise physiological processes in partners (e. g. gonad maturation, Diamond & Terborgh, 1968; Harcus, 1977), or facilitate recognition of partners (Todt, 1970). In the Polynesian megapode, duetting after mates became separated might also help finding each other. At dusk, in dim

light, the duet might help to go to roost at the same time and in close approximation. During the night, when the megapodes do not react to playback, the duet seems to serve pair-bonding.

The idea of a mainly territorial function of song and duet in the Polynesian megapode is supported by: (1) Both vocalizations are too loud to be directed only towards the mate (Seibt & Wickler, 1977). (2) If the song or duet was only directed towards the partner, visual courtship displays should also take place. Its absence seems to show that both sounds are also an acoustic signal towards neighbours (Seibt & Wickler, 1977). (3) "Counter calls" are used during territorial disputes in many animals (Thorpe, 1972; Kunkel, 1974; Todt, 1975; Harcus, 1977; Seibt & Wickler, 1977). (4) The vigorous response of Polynesian megapodes to playback of song and duet is likely to serve either announcing or defending a territory (Seibt & Wickler, 1977). The agonistic nature of song and duet is also indicated by the responsiveness to playbacks being restricted to the daytime, the only time when territorial disputes occur.

A duet might not only advertise an occupied territory but also an existing pair-bond, so that potential intruders are discouraged from entering the territory in search of mates (Farabaugh, 1982; Wickler & Seibt, 1980). The "counter-songs" or "counter-duets" between neighbouring pairs may be a form of ritualised fighting, since they help to solidify the borders of a territory with a low risk of injury.

The differences between the songs of males seem permanent and characteristic for individual males, since they were maintained during the 17-months study period. This will facilitate communication between partners (Diamond & Terborgh, 1968). It is also an advantage to rivals, who have to answer the calls of their well-known neighbours less frequently and thus save energy (Thorpe, 1961; Galeotti & Pavan, 1993). Interindividual differences between male songs also occur in the Nicobar megapode *Megapodius nicobariensis* Blyth, 1864 (R. Sankaran, pers. comm.).

The whistles have to be regarded as alarm calls, since they often occur in situations in which the megapodes were disturbed. Weir (1973) and Todd (1983) mention these calls but did not allude to their signal function. In case the intruder is hidden and not visible to the megapodes, it is always the male who approaches this source of disturbance and whistles. He thereby seems to alert the female to the threat (this is probably what Glass, 1988, calls "curiosity calls" in the Micronesian megapode, *Megapodius laperouse* Gaimard, 1823). When a pair is disturbed by an observer, it is mostly the male who utters whistles as alarm calls first; these sounds therefore serve a mate guarding function. Additionally they might sometimes have a pair-coordinating function when both partners flee from the observer and whistle at the same time.

The function of clucking is not yet clear, although it might assist to maintain pair contact.

Comparison with other megapodes

Not much is known about the vocalization of *Megapodius* species and for most sounds it is not even known by which sex they are produced. In two of the better studied species, the Micronesian and orange-footed megapode, the sound repertoire seems similar to that of the Polynesian megapode.

Duets are known for all *Megapodius* species (S. Birks pers. comm. for the Vanuatu megapode *M. layardi* Tristram, 1879, R. Sinclair pers. comm. for the New Guinea

megapode *M. decollatus* Outstalet, 1878, R. Sankaran pers. comm. for the Nicobar megapode, Coates & Bishop, 1997, for the Tanimbar megapode *M. tenimberensis* Sclater, 1883, Jones et al., 1995, for other species) except the Philippine megapode, *M. cumingii* Dillwyn, 1853. T. O`Brien and M. Kinniard (pers. comm.), who worked in North Sulawesi for some years don't recall ever having heard Philippine megapodes duetting. In all other species the duet seems similar to that of the Polynesian megapode: one partner starts and the other joins in shortly after so that both call simultaneously (New Guinea megapode, Gilliard & LeCroy, 1966; orange-footed megapode, Crome & Brown, 1979; Micronesian megapode, Glass, 1988; Nicobar megapode, R. Sankaran, pers. comm.; all other species Jones et al., 1995; p. 177, 188, 197, 202). In four species, the male is assumed to initiate the duet (dusky megapode *M. freycinet* Gaimard, 1823, Forsten's megapode *M. forsteni* G. R. Gray, 1847, orange-footed and New Guinea megapode, Jones et al., 1995; p. 187, 196, 202 & 212), whereas in the Micronesian and Sula megapode *M. bernsteinii* Schlegel, 1866, it is said to be the female (Glass, 1988; Jones et al., 1995; p. 177). Probably both sexes can start the duet in all these species, as in the Polynesian megapode, the Nicobar megapode (R. Sankaran, pers. comm.) and the orange-footed megapode, in which the female joins in after the male early in the year but largely becomes the initiating partner towards the breeding season (Crome & Brown, 1979). In this case, the female's motivation to initiate the duet might be her increasing readiness for egg laying. In the female Polynesian megapode, one motivation for starting a duet might be the willingness to defend the territory during playback.

As in the Polynesian megapode, the male part of the duet also occurs as song by itself in the Micronesian, orange-footed and Nicobar megapode (Glass, 1988; Crome & Brown, 1979; R. Sankaran, pers. comm.). Its function is also assumed to be territorial. In all these species neighbouring pairs respond to each other, similar to the "counter-calls" of the Polynesian megapode. In the orange-footed and Micronesian megapode, the female contribution to the duet is also given in isolation, mostly during agonistic interactions at the laying burrow (Crome & Brown, 1979; Glass, 1988).

Additional sounds known so far are alarm calls in the orange-footed, Micronesian and Philippine megapode (Crome & Brown, 1979; Glass, 1988; Firman, 1995). They might resemble the whistles of the Polynesian megapode. Its soft cluck might have a similar function as those vocalizations described as "soft contact calls between partners" in the Micronesian, Vanuatu and Nicobar megapode (Glass, 1988; Bregulla, 1992, Jones et al., 1995).

For the other megapode taxa the following sounds have been described: malleefowl perform duets (Frith, 1959; Immelmann & Böhner, 1984) which can be initiated by both partners (Böhner & Immelmann, 1987). They assume a mainly pair-bonding function for these monogamous birds. Probably also the black-billed talegalla *Talegalla fuscirostris* Salvadori, 1877, in which "a pair sometimes calls together" has a duet (Jones et al., 1995). The reason for the absence of duets in the remaining species could be either promiscuity as, for example, in the Australian brush-turkey (Jones, 1990), the absence of (feeding) territories or lack of reliable data.

Additional sounds that occur in other megapodes include: whistles or similar alarm calls (Frith, 1959; Ripley, 1964; Coates, 1985), calls of unknown signal value of the male (Bellchambers, 1916; Kloska & Nicolai, 1988) and contact calls (Frith, 1959; Coates, 1985; Jones, 1987).

The "distress calls" of the Polynesian megapode chick are the first known sounds of any *Megapodius* chicks. Chicks of the red-billed talegalla, *Talegalla cuvieri* Lesson, 1828, and the Moluccan megapode, *Eulipoa wallacei* G. R. Gray, 1860, utter no calls in aviaries (Bergman, 1961; West et al., 1981). Young malleefowl remained silent in the aviary, whilst in the hand they uttered a "deep grunting" (Frith, 1962). When disturbed, chicks of the Australian brush-turkey "coo"-ed and answered with cooing sounds to other chicks (Baltin, 1969); among 50 chicks only one uttered a "coo" when handled (S. Birks in Jones et al., 1995). Chicks of the maleo *Macrocephalon maleo* S. Müller, 1846, uttered a "kuk" when held in the hand. One 12 day old chick was heard calling almost like the rolling call of the male, though softer (Jones et al., 1995). In the field, Frith (1959) observed three chicks of the malleefowl uttering a grunt when hatching from the mound; many other chicks then remained silent.

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