Aggressive interactions and intermale spacing in choruses of the leaf-folding frog, *Afrixalus delicatus*

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Intermale spacing was examined in caged *Afrixalus delicatus* choruses. Males maintained an individual distance using an advertisement call, an encounter call and physical combat (or the threat of combat). An increase from low to intermediate chorus size (2–4 males) led to a decrease in nearest calling neighbour distances. At high chorus sizes (5–8 males) males maintained a minimum individual distance of 30–35 cm. New calling males were not accommodated in the chorus once eight males were calling. As the chorus size increased, a greater number of aggressive interactions were required to maintain the minimum distance. The spatial separation of calling males reduces the number of competitors when space is limited. The maintenance of a preferred minimum individual distance may increase a male's reproductive success by reducing acoustic interference with neighbouring males as well as providing a clear pathway for female approach.

Spasiëring tussen *Afrixalus delicatus*-mannetjiekoorgroepe in hokke is ondersoek. Mannetjies het 'n individuele afstand gehandhaaf deur 'n reklameroep, 'n ontmoetingsroep en fisiese aanranding (of die dreiging daarvan) te gebruik. 'n Toename vanaf lae na intermediêre koorgrootte (2–4 mannetjies) het aanleiding gegee tot 'n afname in naaste-buurmanroepafstand. By hoër koorgrootte (5–8 mannetjies) het mannetjies 'n minimum indiwiduele afstand van 30–35 cm gehandhaaf. By groepe groter as agt mannetjies is nuwe mannetjies nie in die koor geakkommodeer nie. Soos die koordigtheid toegeneem het is 'n groter aantal aggresiewe interaksies benodig om die minimumafstand te handhaaf. Wanneer spasie beperk is, tree die ruimtelike skeiding van roepende mannetjies op om die aantal mededingers laag te hou. Die handhawing van 'n verkose minimum indiwiduele afstand lei miskien tot 'n hoë mate van manlike voorplantingssukses deurdat akoestiese steurnis van buur-mannetjies gereduseer word en dat 'n duidelike weg vir die naderkom deur wyfies verskaf word.

In prolonged breeding anurans, a male's reproductive success depends on his ability to attract females to his calling site and to prevent interference from other males (Wells 1977). The maintenance of an individual distance may increase a male's reproductive success in three ways: it may enable females to locate individual males more easily by reducing acoustic interference between callers (Whitney & Krebs 1975); it may reduce the number of competitors by preventing new males from calling (Wells 1977); and it may provide a clear pathway for female approach (Whitney & Krebs 1975) Males are therefore under selective pressure to maintain adequate spatial separation (Telford 1985).

Male spacing is well documented in prolonged-breeding anurans (Arak 1983; Crump 1972; Fellers 1979; Whitney 1980). Apart from attracting mates, the advertisement call may inhibit calling by nearby males (Whitney & Krebs 1975) and, through mutual avoidance, function in the initial spacing of calling males (Gerhardt 1975; Ryan 1982; Telford 1985; Wells 1977). Encounter calls and physical combat also play an important role in the agonistic behaviour required to maintain spatial organization (Arak 1983; Bunnel 1973; Fellers 1979; Schwartz & Wells 1985; Whitney 1980).

The distance between each male and its nearest calling neighbour has been used as an index of spatial separation within anuran choruses (Awbrey 1978; Dyson 1986; Fellers 1979; Robertson 1984; Rosen & Lemon 1974 and others). In many species, nearest neighbour distances initially decrease with an increase in chorus density (Dyson 1986; Fellers 1979), but males maintain a specific minimum inter-individual distance at high densities. This often results in an even distribution of calling males in the chorus (Dyson 1986; Fellers 1979; Robertson 1984).

Afrixalus delicatus is a small, non-territorial, prolonged-breeding frog (snout-vent length ranges from 15–22 mm). Males call from stationary sites but oviposition does not occur at the call site and there is no resource defence by males (Backwell 1987). This paper examines the nature of male–male aggressive interactions and the role of social behaviour in intermale spacing, as well as the effects of chorus density on the nearest neighbour distances and on the frequency of aggressive interactions required to maintain the minimum inter-individual distance.

Methods

The study was conducted on a caged population of males. The cage (2 × 3 × 2 m) was a wooden frame covered in polypropylene netting. Access was through a sealed canvas door. An artificial pond (1 × 2,5 × 0,5 m) was dug in the cage. Vegetation from the natural breeding area was transplanted to the pond and included *Polygonum pulchrum* and *Ludwegia stolonifera,* the plant species favoured by *A. delicatus* as calling sites (Backwell 1987). The plants were evenly distributed throughout the artificial pond. The cage was illuminated with a 60 W red light bulb suspended 1,5 m above water level. Calling males were collected from shallow coastal pans near Mtunzini, Zululand (28°051'S / 31°46'E) and

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transported approximately 6 km to the cage. The number of males calling in the cage was controlled by adding or removing males and a stable chorus was established, usually after two nights.

Maintenance of spacing

Caged choruses were observed during the 1985–1986 breeding season (October–February). Aggressive interactions were observed from either the initial approach of

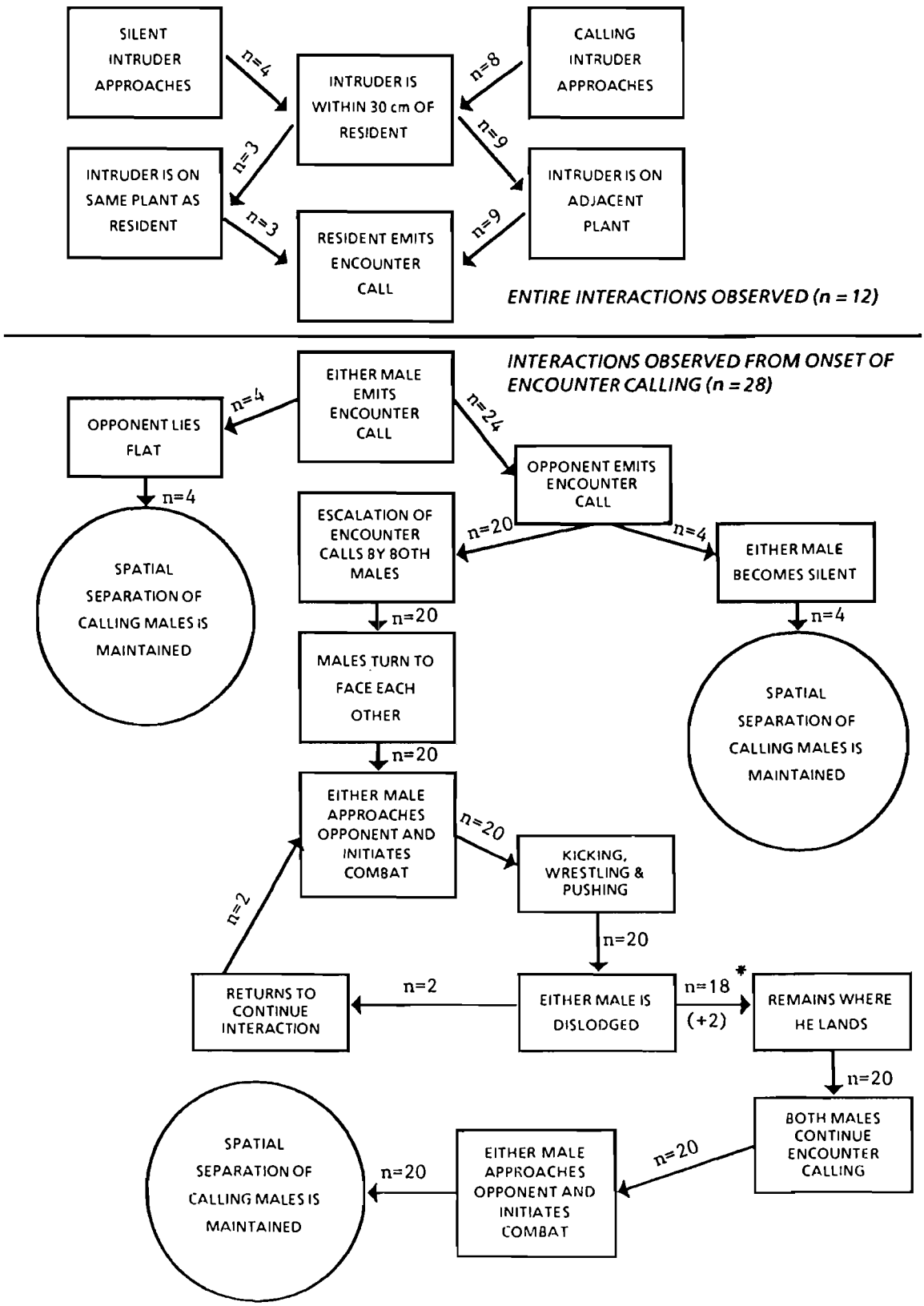

Figure 1 Flow diagram of aggressive interactions between *A. delicatus* males. * Eighteen of the dislodged males remained where they landed, while two males returned to continue the interaction, after which the dislodged males then remained where they landed.

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the intruding male, or the onset of encounter calling by either of the males. The spatial positions of the males, their movements, vocal interactions, and the form of physical combat were documented. Time measurements were made using a stopwatch, and the outcome of the interactions was noted with reference to the positions of the two males before and after the interaction.

Effect of density on spacing

The shortest distance from each male to its nearest calling neighbour was measured for five choruses at each of seven chorus sizes (2–8 calling males). The measurements were made to the nearest centimetre using a 3-m tape. Each chorus size was replicated with new groups of frogs on different nights. A multiplicative regression analysis and a one-way analysis of variance were performed on the data. A Student-Newman-Kuels test was used to calculate the significance levels of the differences between the mean nearest neighbour distances of each chorus size.

A second experiment was conducted over the 1984–1985 and 1985–1986 breeding seasons. Nearest neighbour distances were measured (as above) on five occasions at each of three chorus sizes (3, 5 and 8 males), the number of encounter calls and physical aggressive interactions were counted in each of the choruses over a 30-min period. Readings were always taken between 21h00 and 22h00 to avoid the possible influence of time of night, which has been shown to affect the level of aggression in a sympatric species, *Hyperolius marmoratus* (Dyson 1986). A one-way analysis of variance was conducted on the data.

Results

Maintenance of spacing

In all of the 28 aggressive interactions (12 observed from the initial approach of the intruder and a further 16 from the onset of encounter calling), aggressive vocalization preceded physical combat. Initially the encounter calls of both males were interspersed between advertisement calls, but later males ceased advertisement calling and emitted only encounter calls. The data for all interactions involved in the maintenance of spacing are presented in Figure 1. Interacting males were always found at least 40 cm apart after an interaction, and always further removed from each other than before the interaction. Aggressive interactions lasted between 0,5–3,5 min, although physical combat was shorter, lasting 0,5–2,5 min.

Effect of density on spacing

Increase in chorus size was accompanied by a decrease in nearest neighbour distances ($r_m = 0{,}97$; $df = 6$; $p < 0{,}01$) (Table 1). One-way analysis of variance revealed a significant difference between the overall mean nearest neighbour distances for all chorus sizes ($F = 12{,}77$; $df_{num} = 6$; $df_{den} = 168$; $p < 0{,}01$). A Student-Newman-Kuels test revealed that there are non-significant differences between the nearest neighbour distances in choruses of 5, 6, 7 and 8 males, but that significant differences exist between the nearest neighbour distances in chorus of 2, 3 and 4 males as well as between these low chorus densities and all other choruses (see Table 2). As the chorus density increased, the number of vocal and physical aggressive interactions increased ($F = 13{,}40$; $df_{num} = 2$; $df_{den} = 12$; $p < 0{,}01$) (Table 3).

Table 1 Nearest neighbour distances (NND) at different chorus sizes (CS)

CS	n	$\bar{x}$ NND cm	SD
2	10	88,2	15,3
3	15	67,7	33,3
4	20	52,8	29,3
5	25	33,4	20,1
6	30	35,7	26,0
7	35	31,7	24,9
8	40	31,3	18,9

Table 2 Student-Newman-Kuels analysis between mean nearest neighbour distances at different chorus sizes

Chorus size	Chorus size 2	3	4	5	6	7
3	0,01					
4	0,01	0,05				
5	0,01	0,01	0,05			
6	0,01	0,01	0,05	NS		
7	0,01	0,01	0,05	NS	NS	
8	0,01	0,01	0,05	NS	NS	NS

Table 3 Effect of nearest neighbour distance (NND) on the frequency of aggressive interactions (FAI) over a 30-min period

CS	$(N)n$	$\bar{x}$ NND cm	FAI	SD
3	(5)15	59,4	0,0	0,00
5	(5)25	39,4	0,4	0,55
8	(5)40	28,9	1,8	0,84

n = number of individuals
N = number of choruses.

Discussion

Spatial separation between calling males is maintained in *A. delicatus* choruses. The advertisement call presumably functions in the initial separation of calling males (see Backwell 1988 for additional information on the functional partitioning of the two-part advertisement call). The encounter call is emitted during aggressive interactions, and together with physical combat, or the threat of combat, maintains the spatial separation

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between callers. The form of combat in *A. delicatus* is similar to that found in other frogs (Bunnel 1973; Fellers 1979; Telford 1982; Wells 1977) and involves wrestling, kicking and pushing.

The distance between each male and its nearest calling neighbour decreased with an increase in chorus size up to a point, and males then defend an individual distance of approximately 30–35 cm. At low sizes (2–4 males), males were spaced maximally, or at least rarely less than 30 cm apart, and very few aggressive interactions occured between them. At higher chorus sizes (5–8 males) aggressive interactions are required to maintain a preferred minimum individual distance. As the chorus size increases, more aggressive interactions are required to maintain this distance. Choruses of nine or more males were extremely rare in the cage (found only on three occassions irrespective of the number of males present, n = approximately 200). It is proposed that at a chorus size of eight males, no more males were accommodated in the chorus and additional males were inhibited from calling.

The spacing behaviour exhibited by *A. delicatus* appears to reflect the ability of males to limit the number of competitors, but only when space becomes limited (Fellers 1979; Wells 1977). Under natural breeding conditions, space is not limited and additional males could be accommodated on the perimeter of the chorus. The reduction of competition may therefore be an effect of the maintenance of spacing under certain natural conditions (e.g. at a small breeding pond where space is limited). Wells (1977) proposed that the maintenance of spacing would reduce competition, even under conditions of unlimited space, since newly arrived males would have to search for calling sites at suitable distances from other males, and in so doing, would loose valuable mate-attraction time. The extent to which this would affect a resident male's reproductive success in *A. delicatus* is questionable.

The probable function of spacing in this species is in the increased male reproductive success gained through: (i) the decrease of acoustic interference between near neighbours (Whitney & Krebs 1975) which results in an increase in a male's locatability and the distinctiveness of his call; and (ii) the provision of a clear pathway for female approach (Whitney & Krebs 1975) which prevents neighbouring males from intercepting approaching females.

Telford (1982, 1985) postulated that spacing evolved as a result of the limited resolving powers of the female auditory system. He experimentally demonstrated that there is a selective advantage to males in maintaining a preferred minimum individual distance in *Hyperolius marmoratus* since females discriminated against calls broadcast from sources less than 50 cm apart. He also found that, although females preferred widely-spaced calls, they were still able to locate individuals that were less than 50 cm apart. This suggests that, at high chorus densities, males should invest more time in calling and tolerate neighbours at closer distances up to the point where the advantages of being spatially separated are matched by the disadvantages of spending increased time in aggressive interactions (Dyson 1986; Telford 1985). Dyson (1986) found that additional males could be accommodated in *H. marmoratus* choruses since no minimum individual distance was maintained (Blackwell 1987), thus there may be a compromise between spacing and the time spent on aggression. However, in *A. delicatus*, the advantage of being spatially separated outweighs the disadvantage of spending increased time in aggressive interactions at all chorus densities, and no compromise is made.

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