PRIMATES, 38(3): 281–291, July 1997

Dyadic Associations of Red Colobus and Diana Monkey Groups in the Taï National Park, Ivory Coast

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ABSTRACT. Members of the genus Colobus have been observed to associate frequently with Cercopithecus monkeys in several African sites. In the Taï National Park, Ivory Coast, one group of western red colobus was found to be in association with one particular group of diana monkeys more than could be expected by chance (HOLENWEG et al., 1996). We show that dyadic association is not an idiosyncrasy of these two groups, but rather a pattern that is general for our study site. All five red colobus groups we studied were closely associated with diana monkeys during more than 60% of the time. Four groups had one particular diana partner group, the fifth two different partners. Apart from the red colobus, three more primate species, the olive colobus, Campbell's monkey, and the lesser spot-nosed monkey, were also strongly attracted to diana monkeys.

Key Words: Colobus; Cercopithecus; Polyspecific association; Cooperation; Mutualism.

INTRODUCTION

Mixed-species associations among primates are widespread and have been reported from tropical forests of Africa (GAUTIER & GAUTIER-HION, 1969; STRUHSAKER, 1978, 1981; GAUTIER-HION et al., 1983; GALAT & GALAT-LUONG, 1985; CORDS, 1987, 1990a, b; WHITESIDES, 1989; OATES & WHITESIDES, 1990; MCGRAW, 1994) and South America (TERBORGH, 1983, 1990; GARBER, 1988; HEYMANN, 1990; PERES, 1992a, b). A number of different types of associations have been described, ranging from chance encounters and temporary assemblies of two or more species to permanent bispecific groups. Within any community the composition of associations tends to be quite consistent. Some species combinations habitually form polyspecific associations, while other combinations never do (TERBORGH, 1990).

Polyspecific associations can be formed, either because primate groups meet each other by chance, or because groups actively seek the company of allospecifics. Chance encounters, which can take place randomly either independently of resources throughout the range, or mainly at commonly used resources, do not ask for a functional explanation. The question of an ultimate cause can be asked when members of one species are apparently directly attracted by groups of other species. Two such causes have been proposed: improved acquisition of resources, and better protection against predation. For a more extensive discussion, see BSHARY (1995), HOLENWEG et al. (1996), and WACHTER et al. (1997).

In the Taï National Park in Ivory Coast, West Africa, one group of red colobus monkeys (*Colobus badius*) was found to associate considerably more with diana monkeys (*Cercopithecus diana*) than would be expected as a result of chance encounters alone (HOLENWEG et al., 1996). The red colobus group was found to associate almost exclusively with one specific diana monkey group, with which it shared its range. The associations between these groups did not result from meetings at common resources and could not be explained in terms of foraging benefits (WACHTER et al., 1997). Observational and experimental evidence showed that red colobus seek the company of diana monkeys under increased predation pressure from chimpanzees (NOË & BSHARY, 1997) and that both species are less vigilant and more exposed in each other's company (BSHARY, 1995; BSHARY & NOË, in press). These findings support the hypothesis that reduction of predation pressure is the ultimate cause for the associations of red colobus and diana monkeys in Taï. These conclusions, however, were based on observations on a single pair of groups only.

In this study data on the polyspecific associations of four additional red colobus groups, and the diana monkey groups they were regularly associated with, are presented. Our primary aim was to establish whether the pattern of association found for the first red colobus – diana combination (HOLENWEG et al., 1996; WACHTER et al., 1997) is an idiosyncrasy or typical for the study area. The finding that this pattern is common in the area generates further questions: Can we envisage how such a system of pairwise associated groups originated? What are the causal relationships between groups density, range size, group size, and the association pattern? Diana groups are estimated to occur in higher densities than red colobus groups, and the range of our first diana monkey group was larger than that of it's partner group (HOLENWEG et al., 1996). In a system with strict pair formation between groups, this would imply that either some diana groups are without partners, or that some red colobus groups have more than one partner. In addition, one would expect neighbouring groups of diana monkeys to have more extensive overlaps than neighbouring red colobus groups. We present data on intra- and inter-specific range overlaps and calculate an alternative estimate of group densities on the basis of these data. Finally, we ask whether the pattern of association of red colobus monkeys with primate species other than diana monkeys is also similar for all red colobus groups.

METHODS

STUDY SITE

The study area lies about 20 km south-east of the town Taï in the south-west Ivory Coast in the Taï National Park, a primary tropical moist forest (definition WHITMORE, 1990) of 4,540 km^2. The following monkey species occur in the Park (nomenclature according to Table A-1 in SMUTS et al., 1987): western red colobus (*Colobus badius*), olive colobus (*C. verus*), western black-and-white colobus (*C. polykomos*), diana monkey (*Cercopithecus diana*), Campbell's monkey (*C. campbelli*), lesser spot-nosed monkey (*C. petaurista*), (greater) spot-nosed monkey (*C. nictitans*), and sooty mangabey (*Cercocebus atys*). *C. nictitans* was not seen in our study area, except for some migrating adult males. Four common predators of monkeys occur in the area: crowned eagle (*Stephanoaetus coronatus*), leopard (*Panthera pardus*), western common chimpanzee (*Pan troglodytes verus*), and man (*Homo sapiens*).

Study Groups

We present data on five different red colobus groups and the diana monkey groups they associated with. Abbreviations and numbers are used to indicate different groups (e.g. Badl, Dia2). The two main red colobus groups, Badl and Bad2, consisted of about 70–75 individuals, each with a median number of 17 adult males and 28 adult females. Our two diana monkey study groups, Dial and Dia2, each had about 25 members, including a single adult male. Habituation of the main study groups had started in February 1991 (Badl and Dial) and in September 1992 (Bad2 and Dia2) respectively. The ranges of these groups were within a grid system with a total area of about 1.7 km^2 demarcated with paint marks on trees at 100 m intervals. The groups Badl, Bad2, Dial, and Dia2 were regularly followed by members of the Taï Monkey Project. For this study we gathered data on three additional groups of red colobus (Bad3, Bad4, and Bad5), and their diana monkey associates. The ranges of these groups were adjacent to those of the main study groups and fell partially in our grid system. These groups were recognized with the help of specific individuals and/or their location relative to neighbouring groups seen or heard simultaneously. We can, however, not present any accurate information about group sizes and group compositions of these groups.

Sampling Methods

The four main study groups, Badl, Bad2, Dial, and Dia2, were continuously followed by different observers over full days (07:00–17:30) or half days (07:00–12:30 or 12:30–17:30) between September 1992 and September 1993 for a total of 2,939 hr 50 min (Badl), 2,342 hr 33 min (Dial), 1,269 hr 19 min (Bad2), and 1,647 hr 40 min (Dia2). Every hour the association state between the focal group and allospecific as well as conspecific groups was recorded, and the location of the center of the focal group was estimated and plotted on a map. In contrast to the four main groups, the additional red colobus groups, Bad3, Bad4, and Bad5, were not followed continually but visited once a week for 20–80 min. During such a visit, the association state between the focal red colobus group and other primate groups was recorded and the location of the center of the red colobus group was estimated and noted.

We used three association states: (1) intermingled (at least one member of one group was within the imaginary polygon formed by connecting the outermost individuals of the other group); (2) adjacent (the distance between the two nearest members of different groups was less than 50 m); and (3) not associated. We noted the exact time of changes in the association state during continuous group follows. Association rates presented are based on the criterion 'intermingled,' except in specific cases mentioned in the text.

Between September 1992 and March 1993 data on Bad2, Bad3, Bad4, and Bad5 were gathered by the first author (OH) and from April through September 1993 by the second author (LL). Observations on Badl, Dial, and Dia2 were mainly done by three assistants: Ferdinand Bélé, Yves Kami, and Georges Koui.

Data Analysis

Association rates, i.e. time in association divided by total observation time, were calculated for the main red colobus study groups and their diana partner groups over periods during which at least one observer was with either group (for Badl × Dial: 3,521 hr 47 min;

for Bad2 × Dia2: 2,420 hr). For Bad3, Bad4, and Bad5 association time was estimated on the basis of the proportion of visits the red colobus group was found in association.

Home range areas were calculated on the basis of location data taken on the hour. The home ranges of Bad1 and Bad2 overlapped with the home ranges of six, respectively five neighbouring red colobus groups. Estimation of the group density of red colobus monkeys was based on the non-overlapping core areas of Bad1 and Bad2, i.e. the exclusive ranges of these groups plus half of the range overlaps with neighbouring groups of conspecifics. The group density of diana monkeys was estimated using the same method. Ranges of Dia1 and Dia2 overlapped with ranges of six and five neighbouring groups of diana monkeys respectively.

RESULTS

Group Densities of Red Colobus and Diana Monkeys

The ranges of the two main *Colobus badius* groups covered an area of 65 ha (Bad1) and 64 ha (Bad2) respectively, the ranges of the two *Cercopithecus diana* partner groups an area of 83 ha (Dia1) and 77 ha (Dia2) respectively. On the basis of these data and estimates of the overlaps of neighbouring conspecifics we could calculate the net area per group: 50.0 ha for Bad1, 51.5 ha for Bad2, 49.0 ha for Dia1, and 48.0 ha for Dia2. This implies an estimated group density of 2.0/km^2 for red colobus and 2.1/km^2 for diana monkeys. The density estimates on the basis of a transect method were somewhat higher: 2.4/km^2 for red colobus and 3.5/km^2 for diana monkeys respectively (Holenweg et al., 1996). The fact that one of our five red colobus groups had two partners (see below) also suggests that the diana groups slightly outnumber the red colobus groups.

Associations Between Partner Groups

Between September 1992 and September 1993 all five study groups of red colobus spent most of their time in association with diana monkeys (Fig. 1). The two main red colobus groups were associated less than 0.5% of their time with any diana monkey group other than their "partner group." Association times of Bad1 and Bad2 with diana monkeys can therefore be viewed as association time with Dia1, respectively Dia2.

Members of the diana monkey groups found in association with Bad3, Bad4, and Bad5 were not individually recognized. We therefore cannot state with certainty whether these red colobus groups also had one exclusive "partner group" of diana monkeys. The fact that we found the five red colobus groups to be associated with a diana group simultaneously on several occasions, supports the idea that there is one particular diana monkey partner group for each red colobus group. In addition, the long-calls of the alpha males of Dia4 and Dia5 were individually recognized and these alpha males were regularly seen and heard in the center of the red colobus groups Bad4 and Bad5 respectively. During our study period the three red colobus groups were each followed over four consecutive days by another member of the Taï Monkey Project. Bad4 and Bad5 consistently followed a single diana group throughout their range, but Bad3 alternated between two diana partner groups (Bshary, pers. comm.). Taken together this strongly suggests that four of the five red colobus groups had a single diana partner group, and one group had two regular partners.

The red colobus group with the lowest association rate we observed, Bad1, was associated

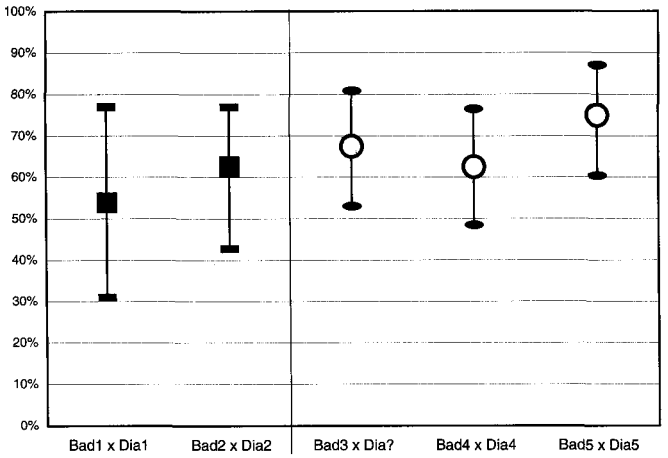

Fig. 1. Associations of five red colobus groups with diana monkeys. For the combinations Bad1 × Dia1 and Bad2 × Dia2 (closed squares) the proportion of time in association is given as a proportion of the total observation time (September 1992 — September 1993). The ranges of monthly proportions observed are indicated by bars. For the other combinations (open circles) the proportion of visits in association is given (40 visits per red colobus group). The bars indicate 95% confidence intervals (according to Table 23 in ROHLF & SOKAL, 1981).

with its diana partner group considerably more than could be explained by chance (HOLENWEG et al., 1996). We conclude that chance encounters could be excluded as a possible explanation for the high association rates of the five red colobus groups with diana monkeys, because the other four red colobus groups were intermingled with their diana partner groups even more than Bad1, and the crucial parameters used in the calculation of the null-model in HOLENWEG et al. (1996) were not obviously different.

OVERLAP BETWEEN HOME RANGES

The overlaps between the home ranges of Bad1 and Dia1 and the ones of Bad2 and Dia2 were found to be extraordinarily large (Fig. 2). Only 2 ha used by Bad1 were never

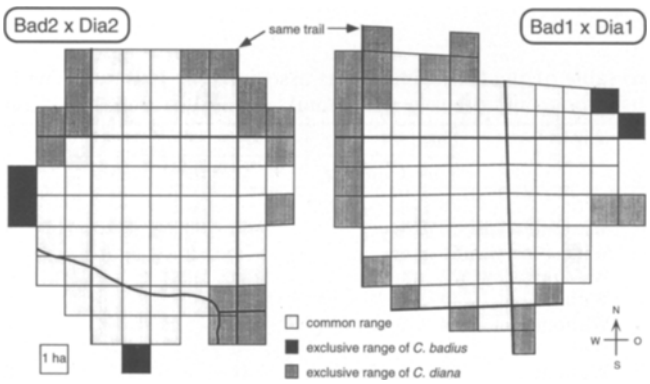

Fig. 2. Home ranges of Bad1 and Dia1, respectively Bad2 and Dia2. The use of squares of 100 × 100 m is indicated for the period September 1992 through September 1993. Bold lines represent trails, thin lines indicate cell boundaries that have been marked with paint only.

visited by Dia1. The remaining 63 ha of the Bad1 home range also formed part of the home range of Dia1. This means that 97% of the Bad1 home range and 76% of the Dia1 home range were used commonly by the two groups. A similar pattern was found for Bad2 and Dia2: between September 1992 and September 1993 the two groups used 61 ha commonly. This made up 95% of the home range of Bad2 and 79% of the home range of Dia2.

DIFFERENCES BETWEEN RED COLOBUS – DIANA COMBINATIONS

As far as association time of red colobus with diana monkeys is concerned, high values were observed for both Bad1 and Bad2 (Fig. 1). However, there were dramatic differences between Bad1 and Bad2 as far as association times with groups of other monkey species are concerned (Table 1). Particularly, groups of *C. verus, C. campbelli*, and *C. petaurista* were regularly seen in association with Bad2, but rarely with Bad1.

Table 1. Percentage of time Bad1, Bad2, Dia1, and Dia2 were associated with the five other monkey species that occur in the study area between September 1992 and September 1993.

	% in association			
Species	Bad1	Bad2	Dia1	Dia2
Colobus verus	0.2	51.6	0.3	94.5
Cercopithecus campbelli	6.8	44.4	4.2	88.1
Cercopithecus petaurista	8.6	31.2	12.1	54.7
Colobus polykomos	3.2	2.6	31.1	28.4
Cercocebus atys	5.0	4.0	9.6	9.7

Total observation time of Bad1: 2,939 hr 50 min; Bad2: 1,269 hr 19 min; Dia1: 2,342 hr 33 min; Dia2: 1,647 hr 40 min.

Data on the associations of the diana monkey groups with other species explain this observation (Table 1). All three species mentioned above were associated for a considerable proportion of the time with Dia2. In fact, one group of *C. verus* and one group of *C. campbelli* were almost permanently associated with Dia2 (94.5 and 88.1% respectively). We had the impression that the other monkey species were primarily associated with the diana monkeys and only secondarily with the red colobus. Both the olive colobus group and the group of Campbell's monkeys followed Dia2 (Taï Monkey project, unpubl. data), which automatically lead to frequent associations with Bad2. Dia1 lacked such persistent

Table 2. Two by two table of the times, Bad2 was associated at 14:00 with/without diana monkeys (*C. diana*) and with/without any other species (total number of afternoons considered: 129).

		Bad2		
		With *C. diana*	Without *C. diana*	Fisher exact *p*
C. verus	With	78	1	
	Without	10	40	<0.0001
C. campbelli	With	66	1	
	Without	22	40	<0.0001
C. petaurista	With	44	1	
	Without	44	40	<0.0001
C. polykomos	With	6	0	
	Without	82	41	0.176 (NS)
C. atys	With	8	0	
	Without	80	41	0.055 (NS)

All tests are two-tailed.

Table 3. Two by two table of the number of visits, Bad3, Bad4, and Bad5 spent with/without diana monkeys (*C. diana*) and with/without any other species (total number of visits: 120).

		Bad3		Bad4		Bad5		Total		
		C. diana		*C. diana*		*C. diana*		*C. diana*		
		With	Without	With	Without	With	Without	With	Without	Fisher exact *p*
C. verus	With	3	0	3	0	13	0	19	0	0.007
	Without	24	13	22	15	17	10	63	38	
C. campbelli	With	3	0	11	2	8	0	22	2	0.006
	Without	24	13	14	13	22	10	60	36	
C. petaurista	With	7	1	8	1	6	0	21	2	0.011
	Without	20	12	17	14	24	10	61	36	
C. polykomos	With	1	0	0	0	2	0	3	0	0.551 (NS)
	Without	26	13	25	15	28	10	79	38	
C. atys	With	5	0	4	1	1	0	10	1	0.170 (NS)
	Without	22	13	21	14	29	10	72	37	

All tests are two-tailed.

followers during our study period. To verify this impression we tested, whether the association of Bad2, Bad3, Bad4, and Bad5 with species other than diana was dependent on the presence of a diana group.

Groups of *C. verus, C. campbelli*, and *C. petaurista*, were found in association with Bad2 significantly more when diana monkeys were present than when diana monkeys were absent. In contrast, groups of *C. polykomos* were not associated more with Bad2 when diana monkeys were present than when diana monkeys were absent. *Cercocebus atys* were more likely to visit the red colobus when diana monkeys where present, but this trend was not significant (Table 2).

In the case of the three red colobus groups we only visited once a week (Bad3 – 5), we did not have enough data to allow the same statistical tests for each group separately. We therefore lumped the data for these three groups (Table 3). Again, the chance to find members of the three species *C. verus, C. campbelli*, and *C. petaurista*, in association with the red colobus groups was significantly higher when diana monkeys were present than when diana monkeys were absent. For *C. polykomos* and *C. atys* we also found the same picture as presented above for the main study groups (Table 3).

DISCUSSION

Association Patterns of Red Colobus and Diana Monkeys

The data presented here show that frequent associations between pairs of red colobus and diana monkey groups are a common phenomenon in our study area in the Taï National Park. One red colobus group (Bad1) investigated between March 1991 and June 1992 was found to form associations with one particular diana group (Dia1) during a considerable proportion of the time, and to share a common range with this partner group (Holenweg et al., 1996). The second intensively studied red colobus group (Bad2) also showed a strong preference for one particular diana group (Dia2) and these groups also shared a common range. Circumstantial evidence suggests that two of the other three red colobus study groups also had their own partner group of diana monkey, while the third probably had two partner groups. The fact that the groups of the two species were not exactly paired

one to one fits our observation that the density of diana groups in our area is somewhat higher than the density of red colobus groups.

Data presented in BSHARY (1995), HOLENWEG et al. (1996), WACHTER et al. (1997), and NOË and BSHARY (1997), show that the ultimate explanation for the associations between red colobus and diana monkeys is predation, and not chance encounters or foraging benefits. Associations of red colobus groups with groups of olive colobus, Campbell's monkeys, as well as lesser spot-nosed monkeys proved to coincide with the presence of diana monkeys (Tables 2 and 3). BSHARY and NOË (in press) show that diana monkeys are preferred as partners on the basis of their quality as sentinels against common predators and are nuclear species in the sense of MOYNIHAN (1962). The habit of diana monkeys of foraging in the thin, outer branches of tree crowns (MCGRAW, 1996) could give them a wider field of vision to scan for predators, than the other species present (cf. MORSE, 1970; SUHONEN et al., 1993, 1994 for tits, *Parus* spp.).

COOPERATION BETWEEN PARTNER GROUPS

We found that red colobus groups tend to be frequently, but not permanently, associated with one specific partner group of diana monkeys. The partner-groups of the two intensively studied combinations had virtually common ranges. We imagine the following scenario leading to this phenomenon: (1) The diets of red colobus and diana monkeys show very little overlap (WACHTER et al., 1997). There will therefore be a severe constraint on the associations, because at least one species will have to deviate from its optimal foraging pattern in order to keep the association intact. This problem could be solved by flexibility in the association formation in reaction to variations in predation risks, when there is enough time to form an association after the perception of the increase in risk, as is especially the case with chimpanzees (NOË & BSHARY, 1997). (2) This conditional strategy will only work if the red colobus have access to their partner group at any time. Only exclusive access will guarantee that the partner group is always available, assuming that conspecific groups do not tolerate each other. This will lead to a distribution of red colobus over the evenly spread resource 'diana monkey groups.' A strong alliance between two specific groups will automatically lead to a strong overlap in home ranges. One group may even defend the core area of the partner group against conspecifics. We would expect the home ranges to be arranged in a concentric way when one species has larger home ranges than the other. In our case almost the entire home ranges of Bad1 and Bad2 are included in the home ranges of Dia1 and Dia2 respectively (Fig. 2). (3) When an area is satiated with the home ranges of two species, each group will overlap with one or more allospecific groups to start with. Competitive conspecific groups usually show small range overlap. If we assume that (a) the home ranges of groups of both species are arranged in a honeycomb way (Fig. 3), (b) home range sizes of groups of the two species are the same, and (c) the two home-range systems are independent of each other, i.e. there are no constraints or 'edge effects' due to topographic structures like rivers or forest edges, then for each group there will be at least one allospecific group with at least 33% overlap. The average group will have a largest overlap with one neighbour of 66%. In reality these chance overlaps between allospecific groups will be even higher, since the ranges of neighbouring conspecific groups overlap. Notably neighbouring diana monkey groups share large parts of their ranges.

One can easily imagine that groups will pair up with the allospecific group they overlap with most, leading to an ideal-free distribution in which groups form pair-wise exclusive

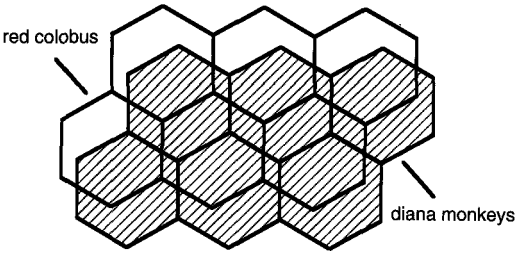

Fig. 3. Hypothetical arrangement of the home ranges of red colobus and diana monkey groups.

associations. An interesting consequence of these pair-wise alliances of allospecific groups is that there is a constraint on group fissions: in the case of a group fission only one of the daughter groups would have a partner group available, unless the partner group splits simultaneously. This may partly explain why the red colobus groups in our area are unusually large for arboreal primates.

CONCLUSIONS

(1) All five red colobus groups we studied in the Taï National Park, Ivory Coast, showed high association rates with diana monkeys. (2) Red colobus groups show a strong preference for one particular diana monkey partner group with which they share a common range. (3) The high association rates between the two species cannot be explained on the basis of chance encounters alone, since the observed values for all five red colobus study groups were considerably higher than the value that can be expected for groups that meet each other by chance alone. (4) The dyadic association between groups of red colobus and diana monkeys constrains the fission of groups.

Acknowledgements. We thank the Ministère d'Enseignement Supérieur et Recherche Scientifique and the Ministère d'Agriculture et Ressources Animales de Côte d'Ivoire for the permission to work in the Parc National de Taï, the Directorate of the Institut d'Écologie Tropicale for the permission to work at the Research Station at Taï and the Sous-Préfèture Taï and the Directorate and Commission of the Centre Suisse de Recherches Scientifiques for the support they gave to our project. This project would not have been possible without the benevolence of the population of the Taï region. We thank especially Dr. OUAYOGODÉ, Dr. SANGARE, Dr. DOSSO, JEAN-MARIE GNAMIEN, BARBARA and PETER LEHMANN, LILIANE and HENRIQUE ORTEGA, HEDWIGE and CHRISTOPHE BOESCH, HANS KUMMER, WOLFGANG WICKLER, and the personel of the IET and the CSRS. FERDINAND BÉLÉ, YVES KAMI, GEORGES KOUI, KATHY HOLENWEG, MARIA SCHABEL, BETTINA WACHTER, KAORU ADACHI, and REDOUAN BSHARY contributed to the fieldwork for the present study. BETTIE SLUIJTER did part of the data analysis. Financial support was provided by the Schweizerische Nationalfonds zur Förderung der wissenschaftlichen Forschung (grant 31-28843.90), the Max-Planck Institut für Verhaltensphysiologie, Seewiesen, Germany, and the C. R. Brupbacher-Fonds.

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—— Received: *September 10, 1996*; Accepted: *February 13, 1997*

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