

Niche differentiation depends on body size in a cichlid fish: a model system of a community structured according to size regularities

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Summary

1. Communities of different species are often structured according to niche differentiation associated with competitive interactions. We show that similar principles may apply on an ecological time-scale when individuals of a species having a wide size variation compete for resources, using the Lake Tanganyika cichlid *Lobochilotes labiatus* (5–30 cm). This species has a mouth especially adapted to suck up invertebrates from rock crevices.
2. Individuals defended feeding territories against similar-sized conspecifics, but not against different-sized ones. Thus, territories of similar-sized fish rarely overlapped, but up to a total of seven individuals (of seven size-ranks) had broadly overlapping territories with dissimilar-sized individuals. Comparison with expectation from the null model demonstrated clearly that observed size ratios between adjacent size rank were determined non-randomly regardless of sexual combinations.
3. Larger individuals took larger prey types of larger average size, but more importantly used wider rock crevices from which to suck food than smaller individuals. We calculated pairwise values of Schoener's index of diet overlap C_d and the values of Levin's index of diet breadth B_d (prey type and prey size) and the same for the width of the rock crevices used for foraging (C_r and B_r). C_d remained high among all combinations of the seven ranks. In contrast, C_r declined strongly in combinations of adjacent ranks (to 0·27), and was low or zero among further different size ranks. This shows that fish with overlapping territories divided the food resources largely through foraging site partitioning. Accordingly, B_d did not depend on the size difference to the nearest two coinhabiting fish, whereas B_r did.
4. We conclude that this *L. labiatus* community is structured non-randomly: body size-dependent effects on foraging site usage result in competition with, and territorial exclusion of, similar-sized individuals, but not of dissimilar-sized individuals that were accepted as coinhabitants. Accordingly, mean body size ratios (large/small) between two adjacent ranks were consistently approximately 1·28 [standard deviation (SD) = 0·07, $n = 104$], while approximately 1·34 from the null model (SD = 0·34, $n = 10\,400$ simulations). We discuss our results as an example of Hutchinson's rule, applied originally to size ratios of different species.

Key-words: competition, food resource partitioning, foraging site partitioning, guild structure, niche differentiation, size ratio.

Introduction

Resource partitioning through size differences between closely related animal species that co-occur in the same habitat may

often shape the structure of a community in terms of biodiversity and densities of the different species, and has received much attention (e.g. Begon, Harper & Townsend 1999). Hutchinson (1959) proposed that many communities may be organized through differences in body size, because body size has a profound impact on resources needed (e.g. diet choice), and

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therefore on resource overlap (e.g. diet overlap) and competition with co-occurring heterospecifics (see also Schlüter 2000a). Hence, this has been the main argument why allopatric twin-species or subspecies show character displacement when occurring sympatrically (Schlüter 2000b), i.e. to avoid competition. There are many examples of regularity in size structure between competitive species within an animal community, although whether the size regularity is determined non-randomly is rarely documented (e.g. Roth 1981; Begon *et al.* 1999).

Less well known is the observation that size ratio may also influence whether conspecific individuals of different sizes co-occur, besides the obvious examples where, e.g. adults use completely different resources compared to their independent offspring (e.g. Buston & Cant 2006). Compelling examples include members of group-living fish competing for food (e.g. Coates 1980; Forrester 1991) and/or competing for the prime breeding positions (e.g. Kuwamura 1984; Sakai & Kohda 1997; Buston 2002; Heg, Bachar & Taborsky 2005; Buston & Cant 2006; Wong *et al.* 2007). In these examples individuals are mainly aggressive against same-sized competitors and may ignore smaller- and larger-sized competitors (Kuwamura 1984; Kondo 1986; Sakai & Kohda 1997; Heg *et al.* 2005). In one fish species, concepts associated with Hutchinson's rule have been applied (Buston 2002; Buston & Cant 2006), and non-random distribution in body size ratio is documented (Buston & Cant 2006). Other examples of size regularity will be from individually territorial fish that share the same home ranges among different-sized conspecifics (e.g. Kuwamura 1984; Kohda & Tanida 1996; Fujita 1997; Sakai & Kohda 1997; Matsumoto 2001), where similar-sized fish defend territories against each other but accept different-sized fish inside their territories, leading to substantial overlap between the territories of dissimilar-sized individuals (Kuwamura 1984; Kohda & Tanida 1996; Fujita 1997; Matsumoto 2001).

Lobochilotes labiatus Boulenger [maximum total length (TL) = 35 cm], a benthophagous cichlid endemic from Lake Tanganyika, is common in the shallow rocky shore around the lake (Kohda *et al.* 1996; Konings 1998). It has been reported that several adult individuals may share the same home range (Kohda & Tanida 1996). Interestingly, our re-examination of *L. labiatus* body size data in the paper by Kohda & Tanida (1996) shows that the mean body size ratio of individuals of adjacent sizes sharing the same feeding area is close to *c.* 1·3 (large-size individual/smaller-size individual). This species utilizes exclusively rock crevices or narrow interstices between pebbles or stones as foraging sites during the daytime (Kohda & Tanida 1996). This species is specialized in sucking small benthic animals from rock crevices using a mouth with thick fleshy lips adapted especially for this purpose (for the convergent evolution of this feature in the Lake Malawi cichlid *Haplochromis euchilus*, see Fryer & Iles 1972). The genus *Lobochilotes* consists of only one species, and no other cichlids in Lake Tanganyika have such thick lips and foraging habits. Feeding fish place their mouth carefully over such crevices and suck up small invertebrates. It has been suggested that the width of the crevices preferred for feeding may depend on mouth size, e.g. due to biomechanical efficiency

and food gain of sucking depending on the difference between mouth size and crevice width (Kohda & Tanida 1996). Because mouth size is expected to correlate allometrically with body size, different-sized *L. labiatus* individuals are expected to partition feeding resources through crevice width preferred for feeding or, alternatively, use similar crevices but suck up different types and sizes of prey species.

It is implied that the foraging pattern of this fish will not be different between sexes (Kohda & Tanida 1996). For the study of size structure, however, it is important to take into account the possibility that there may be two queues in gonochore fish with overlapping territories (a male queue and a female queue) (Buston & Cant 2006). We propose three hypotheses being tested here: (1) that the body size ratio of *Lobochilotes* individuals adjacent in rank that have overlapping territories are distributed non-randomly; (2) that this non-random size structure is a product of generalized competition between all individuals rather than competition between individuals of the same sex; and (3) that this non-random size structure leads to a partitioning of food resources. Hypothesis 1 has a single prediction: that the observed distribution of body size ratios differs from the expected distribution of body size ratios generated by a null model. Hypothesis 2 has two predictions: (i) that the distribution of body size ratios found within sexes does not differ from that found between sexes; and (ii) that indicators of conflict, e.g. proportion of attacks, are equally as common between the sexes as within the sexes. Hypothesis 3 has two predictions: (i) that the resources used vary with body size; and (ii) that as body size ratio increases resource overlap decreases.

Here we report on social structure and resource use and partitioning depending on body size and body size differences in *L. labiatus*. We show that individuals defended feeding territories against similar-sized conspecifics, but not against different-sized ones, with aggression levels falling off rapidly with dissimilarity in size regardless of sexual combination. Thus, territories of up to a total of seven individuals (of seven size-ranks) had broadly overlapping territories with dissimilar-sized individuals. First, we show that size ratios were determined non-randomly regardless of sexual combinations when tested against null models generated by Monte Carlo simulations (Gotelli & Graves 1996; Buston & Cant 2006), and that the non-random distribution is induced by size-dependent social interactions independent of sexes. Then, we analyse the relationships between body size, mouth size and resource usage (prey types and sizes and crevices used for feeding). Subsequently, we test the hypothesis that similar-sized individuals have considerable overlap in resource usage ('resource overlap', Schoener's Index), progressively falling off with dissimilarity in size. We show that the resource overlap is small between individuals sharing the same feeding area due to body size differences, and that the range in resources used ('resource breadth', Levin's Index) depends upon the difference in size between the two nearest-sized competitors sharing the same feeding area. Finally, we discuss our results on conspecific competition vs. body size ratios referring to heterospecific competition vs. body size ratio and Hutchinson's rule.

Materials and methods

FIELD OBSERVATIONS

The field study was conducted at Nkumbla Island near Mpulungu, Zambia at the southern end of Lake Tanganyika from early October to mid-November 2002, using scuba. A study area of 34×28 m with 2×2 -m grids was made on the rocky and sandy bottom at 6–9 m depth, which contained some rocks (< 1 m in diameter), many stones and pebbles. During the course of the study it appeared necessary to extend the quadrat lines to map the large territories of some of the large individuals. In this region, the water temperature in the shallow shore is constant, ranging between 24 and 27 °C during the year. The species composition of the shallow rocky shore is very stable, with only minor between-year fluctuations in numbers (Hori 1997).

Territories of each fish were defined as the outermost of swimming area for foraging, the border corresponding with territorial attacks (Kohda & Tanida 1996). Sexual activities are observed rarely inside territories, in spite of a long-term study period (Kohda & Tanida 1996). Territories of *L. labiatus* contain large numbers of foraging sites (narrow crevices in rocks and interstices between stones), but not refuge sites or shelter holes in many cases (Kohda & Tanida 1996), where territory owners occasionally visit shelters outside their territories when taking a rest or refuge (M. Kohda, personal observation). Territories that are located in areas of high densities of available crevices are significantly smaller than those in areas of low crevice-densities (Kohda & Tanida, unpublished data). These observations suggest that *L. labiatus* defend food or crevices used for foraging but not other resources, such as shelter holes.

All territorial individuals within the study area ($n = 133$) were identified individually and observed from 14 October to 6 November, during which at least nine identified fish disappeared from the study area, of which vacant areas were occupied by similar-sized fish or territory neighbours. Focal individuals were identified by the shapes of the patches on the head and/or cheeks and body sizes (see also Kohda & Tanida 1996). Observations of foraging individuals were made from 1 to 4 m above the bottom, and the presence of the observer did not appear to disturb the fish. Focal individuals larger than 15 cm TL were observed two to six times for 20–50 min, smaller individuals were observed two to four times for 10–20 min. For data of territories, colonizing fish were used ($n = 124$). During each observation the following parameters were recorded: (1) swimming track during foraging; (2) foraging sites (crevice); and (3) all intraspecific interactions and encounters (four categories, see below) with the location mapped in detail and the size of the opponent (see below). The four categories were (each separated for focal or focal received): (3a) ‘attack’, where the focal individual attacked a conspecific or vice versa; (3b) ‘subordinate display’, where the focal fish bent its body and quivered its vertical fins against a conspecific or vice versa; (3c) ‘male courtship display’, where the focal male courted a conspecific or where a focal female was courted by a conspecific; (3d) ‘encounter’, where the focal approached a conspecific, or was approached by a conspecific, within c. 50 cm, but they did not interact with each other. In most cases of social interactions, identification of the opponent was difficult during the observation, but the latter’s estimated body size in comparison with the focal fish was recorded and converted to body size using a calibration in TL mm (see ‘Body measurements and diet’). However, if the opponent’s estimated size and location of the event fitted those of known and captured territorial individuals (coinhabitants or neighbours), these individuals were regarded as such and we used

the measured body size. In the analysis of social interactions, similarly obtained data of some fish outside the study area were also used. In observations of fish, the width of crevices that were used as foraging sites by the focal fish was measured with a ruler (to 1 mm).

BODY MEASUREMENTS AND DIET

After the observation period, of 124 individuals with territories mapped, 72 focal individuals were captured using gill-nets and hand nets (during 6–10 November 2002). Captured fish were killed using an overdose of anaesthetic clove oil. Within 1 h after sampling, the stomach content was fixed by injecting formalin into the abdominal cavity, and individuals were stored in formalin.

For each individual we measured the total length, open mouth width (both to the nearest 0·1 mm) and body mass (0·1 g accuracy) in our laboratory. The estimated total length of focals during behavioural observations and the measured length of these same focals were correlated highly ($R^2 = 0·992$, $P < 0·0001$, $n = 72$). Therefore, we used the estimated body sizes of uncaptured fish throughout in the analyses (i.e. sizes of the 124 – 72 = 52 territory owners not captured). Fish were sexed by gonad examination and by courtship display in some uncaptured fish. Of a total of 113 captured fish, including 41 fish outside the study area, 32 were males, 53 were females and the sex of 28 small fish could not be determined because of immature gonads.

Stomach contents per individual were examined using binoculars (8–20 \times magnification). Prey items were categorized into shrimp (Atyidae, Decapoda), mayfly larvae, midge larvae and caddisfly larvae. Midge and caddisfly larvae were combined because small specimens could not be distinguished from each other. The size of each prey item was measured to the nearest 0·2 mm.

DESCRIPTION OF OVERLAP OF TERRITORIES

The territory arrangement of 124 individuals of *L. labiatus* is shown in Fig. 1. Territories of fish were drawn one by one in approximate size order (from large fish) on the study area map. After the start, several territories rarely overlapped each other and covered the map (e.g. rank A: Fig. 1a). When the territory of a fish overlapped broadly (> 30%) with that of the previous large fish, this fish was grouped into the next small rank (e.g. rank B: Fig. 1b). This procedure was conducted until all territories were drawn.

Territories of the largest fish [size of fish in rank A: mean = 28·7 cm ± 0·71 standard deviation (SD), range = 29·5–27·5 cm, $n = 6$] covered the study area (Fig. 1a). Their territories abutted each other, and overlapped broadly with those of fish of the second rank B that again covered the study area (22·1 cm ± 1·1 SD, 23·0–20·3, $n = 5$; Fig. 1b). Territories of rank B overlapped with those of the third rank C that also covered the substrate (17·5 ± 0·81, 18·5–16·1, $n = 9$; Fig. 1c), and so on. Thus, territories of each rank except the smallest G covered the study area, and territories of different ranks overlapped widely up to six or seven times in total in the order of ranks A, B, C, D (14·5 ± 0·61, 15·9–13·5, $n = 14$), E (11·1 ± 0·68, 12·3–9·9, $n = 28$), F (8·55 ± 0·73, 9·9–7·0, $n = 38$) and G (6·71 ± 0·43, 7·5–6·0, $n = 22$) (Fig. 1). Sizes of fish from adjacent ranks were distinct from one another in all cases, except for the combination of F vs. G, where nine individuals of G were larger than the smallest fish in F.

Rank A fish were all males, rank B and C fish were mainly females, whereas both sexes occurred in all other ranks (Fig. 1).

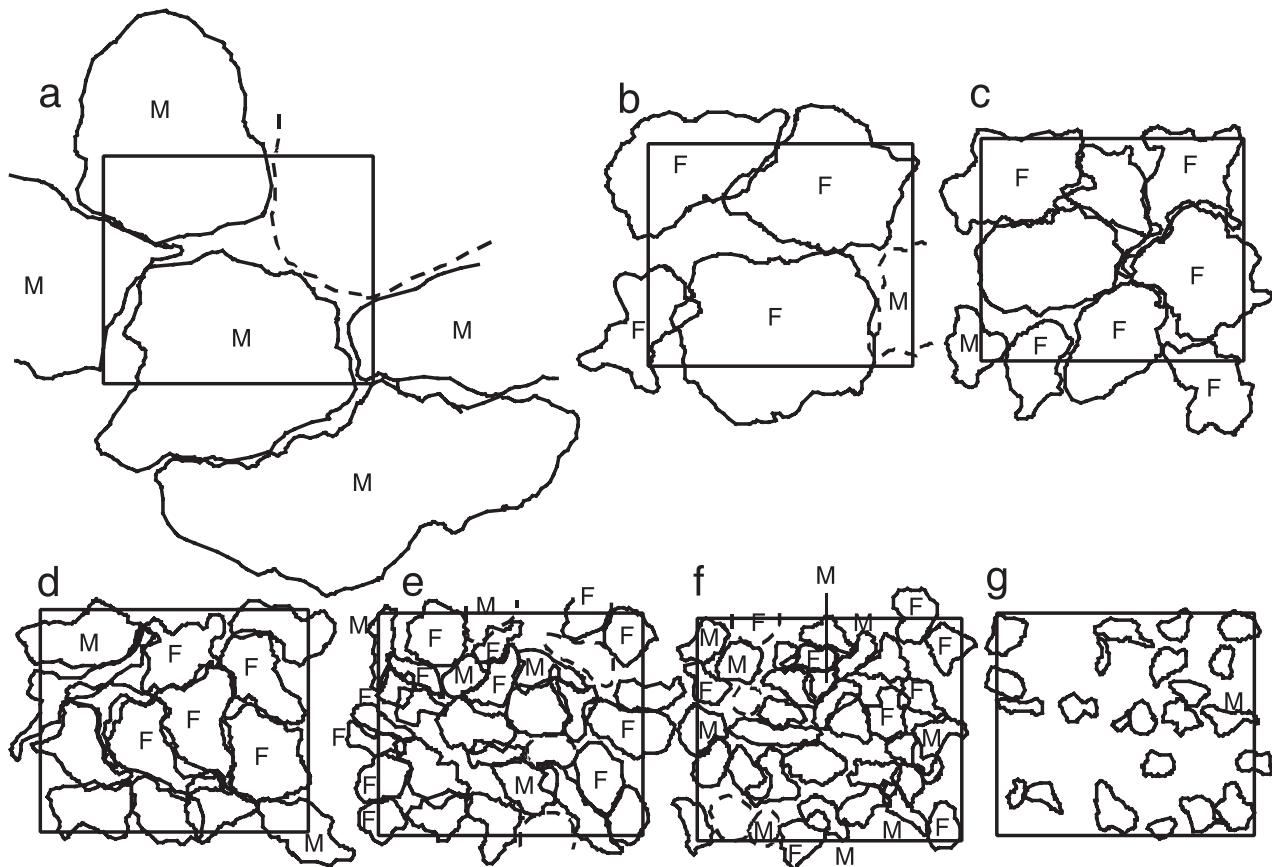


Fig. 1. Territory arrangement of *Lobochilotes labiatus* for each rank [A(a)–G(g)] of fish, with size decreasing from ranks A to G. In each panel the square denotes the boundary of the main study area (34 m × 28 m). F: female, M: male. Solid lines: territory boundaries; broken lines: approximate territory boundaries.

DATA ANALYSES

We tested the hypothesis that body size ratios of individuals that were of adjacent size classes and had overlapping territories are distributed non-randomly (e.g. Hutchinson 1959; MacArthur & Levins 1967). To do so, we compared the observed distribution of size ratios to the distribution of size ratios expected under a null model (Strong *et al.* 1979; Gotelli & Graves 1996; Buston & Cant 2006). We obtained an observed distribution of 104 body size ratios from the map of territory arrangements, in which two adjacent rank fish had overlapping territories: >80% of territories of small fish were covered with territories of large ones (Fig. 1). We created a null model distribution of 10 400 ratios using a Monte Carlo procedure, programmed in Excel. To do this we selected individuals randomly from the 124 available individuals and combined them according to combinations found in the territory map. We then ranked the individuals in these random groups on the basis of relative body size, and calculated the ratio of the body size of individuals adjacent in rank. The procedure was iterated 100 times, generating an expected random distribution of ratios against which our observed distribution could be compared. This model design is appropriate because it excludes only the factor of interest (naturally occurring interactions between individuals adjacent in rank), while incorporating other realistic factors (naturally occurring distribution of body sizes and pattern of territory overlapping) that might influence the results (Gotelli & Graves 1996; Buston & Cant 2006). To examine whether body size ratios within and between the sexes are distributed

non-randomly, the same procedure was performed in female–female combinations (observed ratios $n = 18$, simulated ratios $n = 1587$), in male–male combinations (observed ratios $n = 5$, simulated ratios $n = 530$) and male–female combinations (observed ratios $n = 14$, simulated ratios $n = 1558$).

Prey sizes/types taken and crevice width used for foraging were calculated per focal fish and related to body size. Niche breadth and niche overlap are applied usually to one species and different species, respectively. We applied niche breadth and niche overlap to given-sized groups and different-sized groups of *L. labiatus*. Niche breadths were calculated using index B (Levins 1968):

$$B = 1/(n \sum p_{xi}^2),$$

where p_{xi} is the proportion of one size group x using resource i , and n is the number of resources available. B ranges from $1/n$ (use of a single resource) to 1 (equal usage of resources). Niche overlaps were calculated using the index C (Schoener 1970):

$$C = 1 - 0.5 (\sum |p_{xi} - p_{yi}|),$$

where p_x and p_y are the proportions of size-group x and size-group y .

Statistical analyses were performed using the statistical software program SPSS version 12.0. When data were distributed normally, parametric statistics were performed. When territory sizes were analysed, the values were log-transformed to produce normal distribution. Non-parametric statistics were used for data, which were not normally distributed. All tests were two-tailed.

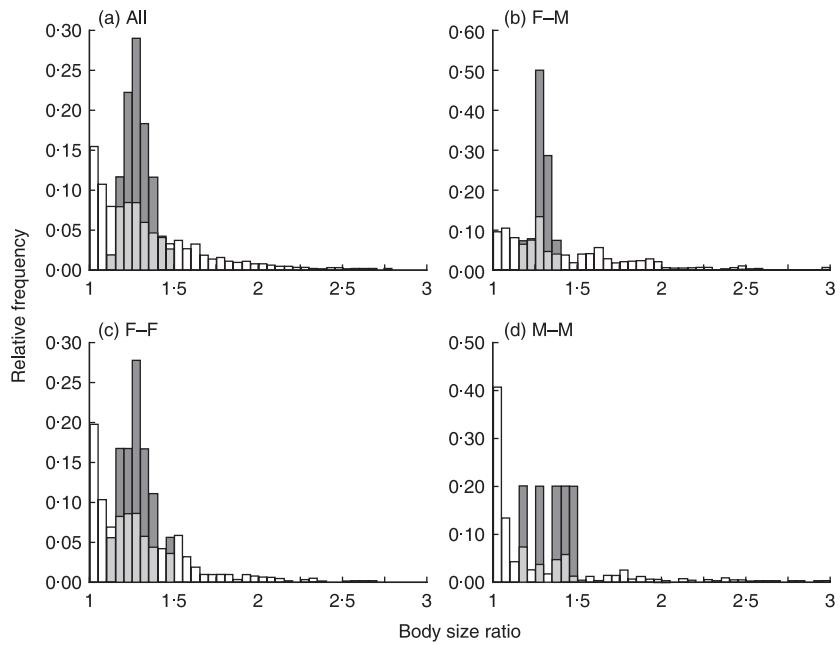


Fig. 2. The observed distribution of ratio of total length (TL) of *Lobochilotes labiatus* individuals that are adjacent in rank and overlap territories (> 80% of territories of the smaller fish) (dark grey and light grey), and distribution of ratios simulated by a null model generated using a Monte Carlo procedure (white and light grey) in (a) all individuals; (b) female–male (F–M); (c) female–female (F–F); and (d) male–male (M–M) combinations. Light grey represents area where two distributions overlap.

Results

NON-RANDOM STRUCTURE OF BODY SIZE RATIOS

The observed distribution of body size ratios in the all pairwise combinations of individuals adjacent in ranks, and thus sharing a feeding area, differed significantly from the distribution of ratios generated by the null model (Kolmogorov–Smirnov test: d.f. = 2, $\chi^2 = 48.33$, $P < 0.0001$, Fig. 2a; observed mean size ratio = 1.28 ± 0.07 SD, $n = 104$, mean size ratio expected under the null model = 1.34 , $n = 10400$). The most striking differences between the distributions are the lack of small and large ratios (e.g. ratio less than 1.1 and more than 1.5) and over-abundance of intermediate ratios (e.g. ratios from 1.15 to 1.40) in the observed distribution (Fig. 2a).

Among sexual combinations, distributions of observed size ratios differed significantly from null-model ratios in female–male (F–M) combinations (d.f. = 2, $\chi^2 = 10.10$, $P < 0.013$, Fig. 2b; observed mean size ratio vs. simulated mean size ratio = 1.28 ± 0.05 , $n = 14$ vs. 1.41 ± 0.37 , $n = 1558$), female–female (F–F) combinations (d.f. = 2, $\chi^2 = 10.16$, $P < 0.013$, Fig. 2c and 1.27 ± 0.09 SD, $n = 18$ vs. 1.29 ± 0.28 , $n = 1587$) and male–male (M–M) combinations (d.f. = 2, $\chi^2 = 8.25$, $P < 0.033$, Fig. 2d and 1.35 ± 0.11 , $n = 5$ vs. 1.28 ± 0.45 , $n = 530$). Again, in the three combinations, the striking differences between the distributions are the lack of small and large ratios (e.g. ratio < 1 : 1 and > 1 : 5) and over-abundance of intermediate ratios (e.g. ratios from 1 : 15 to 1 : 50) in the observed distributions (Fig. 2b,c,d). The observed size ratios were not different among F–F, M–M and F–M pairwise combinations [one-way analysis of variance (ANOVA), $F_{2,34} = 1.82$, $P = 0.18$]. We conclude that the size ratios show non-random aggregation around a value of 1.28 regardless of the combinations of sexes of the fish.

SOCIAL INTERACTIONS

Here we test whether similar-sized *L. labiatus* out-space themselves, whereas dissimilar-sized fish accept each other as coinhabitants. Alternatively, spacing behaviour may depend upon competition for mates rather than body size differences, therefore we examine aggressive interactions depending on body size differences within the males, within the females and between males–females to test whether the body size difference plays a consistent role.

Fish of almost all ranks performed attacks and subordinate displays (Appendix S1 in Supplementary material). Attacks were against fish of the same and one or two lower ranks, whereas subordinate displays were towards fish of the same and one or two higher ranks, and encounters occurred in almost all combinations of ranks except those of the same ranks (Appendix S1). Among fish of the same size ranks, i.e. in many cases territorial neighbours, predominant interactions were aggression, followed by subordinate display (Fig. 3a). Fish among adjacent size ranks performed mainly subordinate display and encounter. Fish among two different ranks performed predominantly encounters followed by subordinate display, and in combinations of more distant ranks fish always ignored each other. Thus, relative rate of ‘dominance interactions’ (the number of attacks plus subordinate displays divided by the number of social interactions plus encounters in percentage), were predominant in fish of the same ranks (93%), followed by adjacent ranks (64%) and two different ranks (32%), and fish in the other combinations showed no agonistic disputes despite encountering each other frequently ($\chi^2 = 300.3$, $P < 0.0001$; Fig. 3a).

Similar patterns of body size-dependent social interactions were observed in female–male (F–M) combinations (Fig. 3b) and female–female (F–F) combinations (Fig. 3c). In F–M combinations, relative rates of the dominance interactions

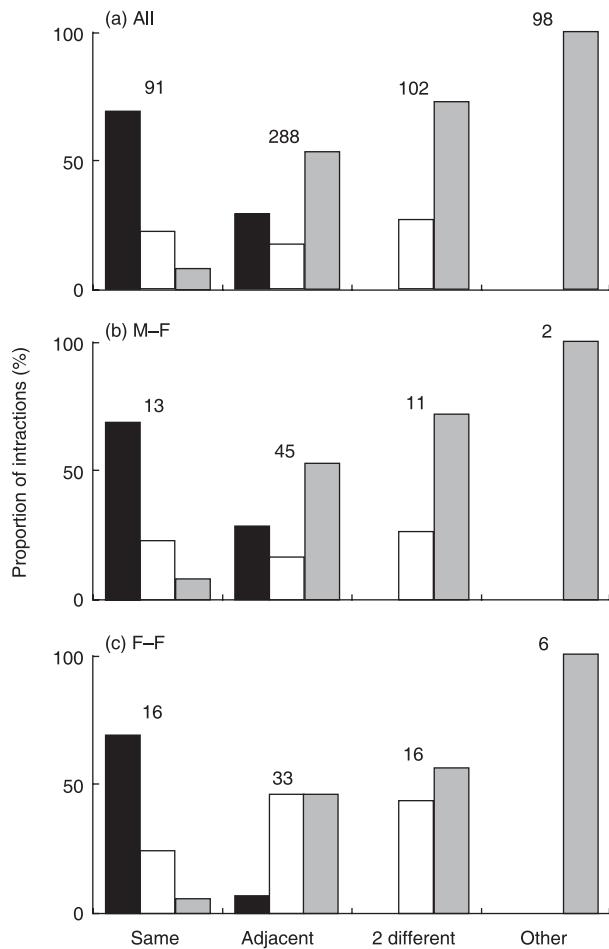


Fig. 3. Proportion (%) of attacks (solid bars), subordinate displays (open bars) and encounters (shaded bars) of the total number of social interactions between fish of same rank, adjacent rank, two different ranks and more than two different ranks (other). Sample sizes, the total number of social interactions, are indicated in the figure. (a) all combinations; (b) female–male (F–M) combination; and (c) female–female (F–F) combination. Male–male combination ($n = 8$) is omitted. Note that all attacks and subordinate displays in adjacent and two different ranks were performed by the larger fish and the smaller fish, respectively.

were predominant in fish of the same ranks (92%), followed by adjacent ranks (47%) and two different ranks (23%) ($\chi^2 = 13.27, P < 0.002$). In F–F combinations, relative rates of the dominance interactions were 94%, 55% and 32% in the same order ($\chi^2 = 14.52$, Yates's correction, $P < 0.001$). In M–M combinations, all were dominant interactions in the same rank ($n = 3$) and adjacent rank ($n = 5$). For all the four combinations, interaction frequency among the rank combinations was not different (log-linear analysis, $\Delta G^2 = 7.01$, Ad.f. = 4, $P = 0.14$).

Courtship interactions were observed in five sexual pairs; three males of rank A courted three females of rank B and two of rank C, and these females all had (partly) overlapping territories with these males. Matured eggs were found in one female of rank B and four of rank C in 37 female samples from the study area.

BODY SIZE AND FORAGING ECOLOGY

Crevices of various widths were scattered over the study area, and each individual fish went from crevice to crevice during a foraging trip within their territories. Stomach contents of *L. labiatus* included shrimps, mayfly, midge and caddisfly larvae consisting of more than 95% of the total number of prey. Small individuals consumed mainly midges and caddisflies, and these were gradually replaced by shrimp for the larger individual *L. labiatus* (Fig. 4a). Mayfly larvae were seldom consumed by any fish. Thus, *L. labiatus* of different sizes foraged on significantly different food types ($\chi^2 = 370.4, P < 0.0001$: size range of 190–215 and 215–240, 240–265 and 265–290 were combined, respectively).

Overall prey size taken correlated with fish size ($R^2 = 0.38, n = 90, P < 0.0001$; Fig. 4b). Open-mouth size was correlated closely with body size ($R^2 = 0.98, P < 0.0001, n = 113$), and was also related strongly to prey size ($R^2 = 0.36, P < 0.0001$). Prey size was not different in function of body size between sexes [analysis of covariance (ANCOVA), full model, sex \times body size: $F_{1,59} = 0.058, P = 0.81$; reduced model, sex: $F_{1,60} = 0.429, P = 0.52$, body size: $F_{1,60} = 33.24, P < 0.0001$].

There was a close match between mean width of the crevices used by each fish and body size of individuals ($R^2 = 0.97, P < 0.0001$; Fig. 4c), and between width of the open mouth of individual fish and crevice size used for foraging ($R^2 = 0.95, P < 0.0001$). Crevice width was not different in function of body size between the sexes (ANCOVA, full model, sex \times body size: $F_{1,36} = 0.244, P = 0.62$; reduced model, sex: $F_{1,37} = 0.289, P = 0.59$, body size: $F_{1,37} = 1060.3, P < 0.0001$). Similarly, log-transformed territory sizes in function of body sizes were not different between the sexes, with the exception of all males of rank A (ANCOVA, full model, sex \times body size, $F_{1,44} = 2.31, P = 0.14$; sex, $F_{1,44} = 1.76, P = 0.19$, body size, $F_{1,44} = 101.9, P < 0.0001$; reduced model, sex: $F_{1,45} = 0.30, P = 0.59$). Thus, there were no differences in crevice size used for foraging and territory size between sexes.

INDICES OF NICHE OVERLAP AND NICHE BREADTH IN SIZE RANKS

Niche overlap indices in prey type and prey size combined (C_d) and in crevice size used for foraging (C_r) were calculated in function of the pairwise body size ratio, where fish (6–29 cm in size) were grouped into 1 cm classes, and C in all combinations with < 4.5 in size ratio were calculated (Fig. 5). C_d was higher between similar-sized fish and declined gradually as the size differences increased progressively, but still remained high even for fish most dissimilar in size (Fig. 5a). In contrast, C_r decreased steeply as the size ratio increased (Fig. 5b). Thus, similar-sized fish are expected to compete for prey types and foraging sites, but as the size difference increases this competition is expected to decrease.

As would be expected from Fig. 5, C_d among size ranks (A–G) still remained high as the rank differed progressively: mean = 0.55 ± 0.16 SD ($n = 5$) between all adjacent ranks but the F–G combination, in which sizes of some fish overlapped,

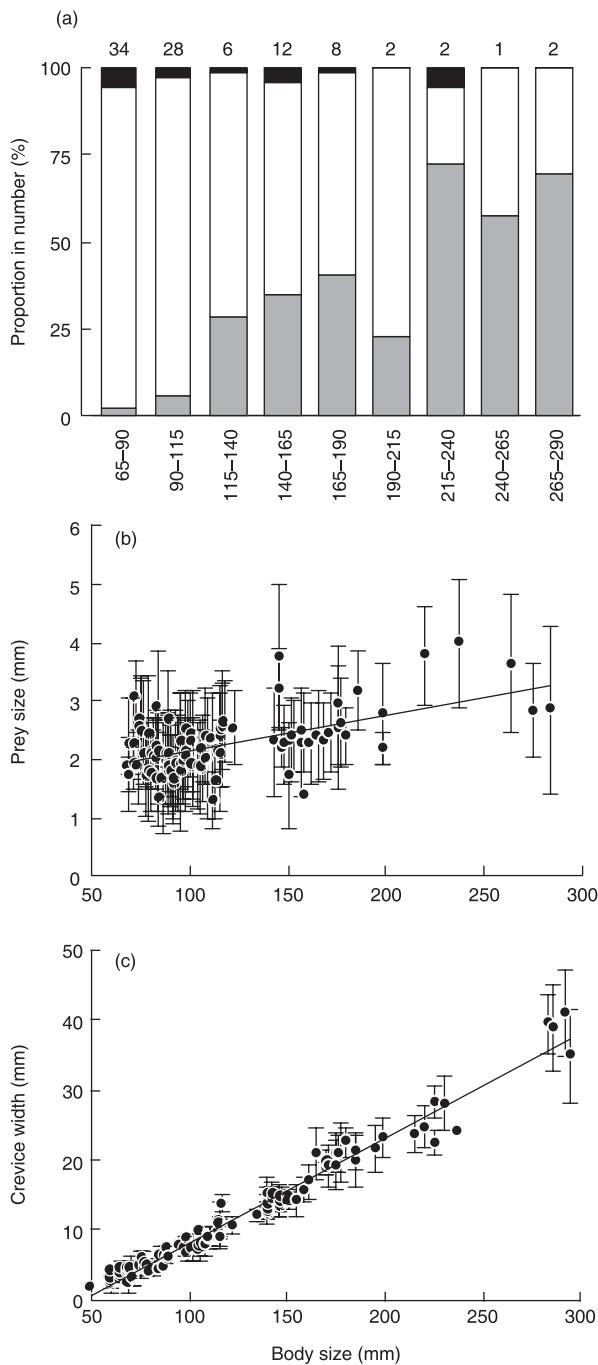


Fig. 4. Relationships between (a) prey items; (b) prey size; and (c) crevice width used for foraging vs. focal body size (total length: TL) of *Lobochilotes labiatus*. (a) Body sizes were lumped in 25-mm TL classes. Mayfly larvae (solid bars), midge and caddisfly larva (open bars) and shrimp (dotted bars), with fish sample sizes given on top of the bars. (b, c) Each dot represents the mean with standard deviation for a focal individual.

0.54 ± 0.10 ($n = 5$) between two different ranks, 0.45 ± 0.10 ($n = 4$) between three different ranks and 0.34 ± 0.05 ($n = 3$) between four different ranks. In contrast, C_r steeply decreased as the size rank differed progressively: mean C_r was 0.27 ± 0.11 SD between adjacent ranks ($n = 5$, if F–G was omitted),

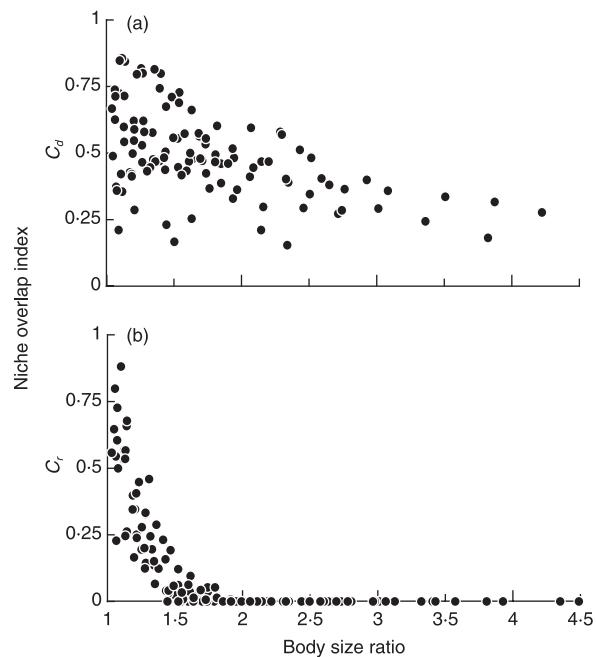


Fig. 5. Pairwise niche overlap indexes in (a) prey item and prey size combined (C_d); and (b) crevice width used for foraging (C_r) in function of the body size ratio [large total length (TL)/small TL] in all individual combinations of *Lobochilotes labiatus*. Fish are grouped into 1-cm TL classes. Plots of fish combinations with sample size of two or more are shown.

Table 1. Niche breadth index (B : Levin 1968) in seven size-ranks in *Lobochilotes labiatus*. (B_d): prey items and prey size, and (B_r): width of crevice for foraging

Size-ranks	B_d	B_r
A	0.20	0.20
B	0.28	0.18
C	0.39	0.18
D	0.33	0.13
E	0.37	0.15
F	0.22	0.12
G	0.20	0.11
Total	1.99	1.07

0.06 ± 0.06 SD between two different ranks ($n = 5$) and close to 0 in further different size-rank combinations.

Niche breadth indices of diet (prey type and size, B_d) and crevice width (B_r) for all size ranks are shown in Table 1. B_d ranged from 0.20 to 0.39 with an average of 0.29 ± 0.08 SD ($n = 7$) and a total of 1.99. B_r ranged 0.11–0.20 with an average of 0.15 ± 0.03 SD ($n = 7$) with a total of 1.07. B_r was significantly smaller than B_d (Wilcoxon's signed-rank test: $Z = 2.20$, $P < 0.027$).

Discussion

Our results show that individual *L. labiatus* defended their territories only against similar-sized fish, with similar-sized fish competing at least indirectly for similar food resources.

Competition for reproductive opportunities does not seem to play an important role for the decision of whether or not to accept coinhabitants, because the frequencies of aggressive interactions were not different between F–M and F–F combinations (Fig. 3). Accordingly, the size ratios in adjacent ranks were not significantly different between F–M and F–F combinations (Fig. 2b,c). Males and females used crevices and took prey depending upon their body size, and defended their territories accordingly against similar-sized fish irrespective of their sex. These observations and some circumstantial evidence (Kohda & Tanida 1996; unpublished data; M. Kohda, personal observation) suggest that the resources defended by *L. labiatus* will be available foraging sites or food but not resources such as shelters, and field experiments with manipulation of food or crevice availability will support this suggestion effectively. The largest males in our study population (rank A) may have had exceptionally large territories for their body size, whose territories were defended vigorously against other large males at least partly to ensure mating with fertile females. Nevertheless, even these males accepted smaller males as coinhabitants.

BODY SIZE AND COMPETITION IN *L. LABIATUS*

Our results show that individual fish used crevices of a very specific width depending on their mouth size. The sucking foraging technique of *L. labiatus* implies that these fish will have difficulty in detecting potential prey visually and selecting prey types and sizes accordingly. Rather, invisible sedentary animals inside silts or fine sand within the crevices are preyed upon, and they are probably sucked up indiscriminately. Various-sized crevices were scattered over the study area, and there was a close match between the size of individual fish and the crevice width used for foraging. It seems plausible that a given-sized foraging fish does not select the prey, but instead selects the crevice conforming to its mouth width, and perhaps a close match between crevice width and mouth width guarantees the largest effectiveness in sucking up invertebrates. This hypothesis needs to be tested in *L. labiatus*, similar to the many studies on optimal choice of prey size depending on the size of the feeding apparatus in a variety of animals (e.g. Zwarts & Blomert 1992; Zwarts, Blomert & Wanink 1992).

The mouth size (and thus body size)-dependent preferences of individual *L. labiatus* for foraging sites and prey show that different-sized fish may partition prey and foraging sites and avoid competition accordingly. The niche overlap indices indicated that as the pairwise body size ratios increased, C_d still remained somewhat higher, but C_r decreased steeply (Fig. 5b). This steep decrement in C_r shows that different-sized fish will partition their foraging sites effectively, and to a lesser extent also their prey. Thus, the larger the difference in size between two individual fish, which can be expressed as a body size ratio, the less competition they can expect between themselves for food. The same- or similar-sized fish (i.e. same rank fish) apparently utilize similar-sized foraging sites with similar prey items and prey sizes, and will not partition foraging sites and food. Thus, as *L. labiatus* is territorial, fish

should maintain territories exclusively against the same- or similar-sized conspecifics but can ignore different-sized fish, regardless of sexual combinations. Indeed, the territory arrangements showed that similar-sized fish maintained territories against each other, whereas different-sized fish overlapped territories widely (up to seven times in our study population). Accordingly, niche overlap indices (C_r) of fish from adjacent ranks for foraging sites were 0.27 on average, suggesting that they partitioned their choice of foraging sites significantly. Territorial aggression against similar-sized fish and tolerance toward smaller-sized coinhabitants inside the territories corresponded with the degree of niche overlap, and we showed that the social relations (dominance, submissiveness) are apparently the proximate factors inducing territory overlaps and coacceptance of two fish. It seems reasonable to assume that focal individuals do not exclude coinhabitants of smaller adjacent ranks because the costs of chasing out these competitors from their territories exceed the costs incremented due to food lost to these competitors (e.g. Robertson 1984; Roberts 1985; Kuwamura 1992; Buston 2004; Wong *et al.* 2007). This assumption needs further experimental verification.

Fish sizes differed between adjacent ranks (except the smallest-sized ranks), and this was reflected in the extent of territory overlap and was distributed non-randomly. Some fish sampled outside the study area fell into the vacant zones in size (M. Kohda, unpublished data) suggesting that, as a regional population, fish size will be distributed continuously, although the size ratio between adjacent ranks will be constant. At least nine fish disappeared from our study area and were replaced by immigrants (within 40 observation days). This means that more than half the fish in one year are expected to disappear ($9/133 \times 365/40 = 0.62$), indicating that the territory arrangements may change dynamically in this population. Despite these dynamics, the regular size difference is apparently maintained non-randomly. We suggest that two major processes may be responsible for this regularity in territoriality depending on body size and body size differences, and accordingly the regularity in body size ratios of adjacent ranks. First, vacant territories are occupied by similar-sized immigrants or territory neighbours. Secondly, larger individuals might regulate the growth of subordinate coinhabitant fish and/or the subordinate regulate their own growth (e.g. one-rank smaller individuals sharing the same foraging area), as has been suggested for group-living fish (Buston 2002, 2003; Heg, Bender & Hamilton 2004; Heg *et al.* 2005; Buston & Cant 2006).

BODY SIZE RATIO AND BETWEEN SPECIES COMPETITION

In guilds of insects, birds and mammals, each species is expected to occupy an ecological niche and, typically, natural selection will either drive closely related species apart in structures related to resource usage, of which body size is a major determinant (character displacement) or force these species to out-space themselves (e.g. differences in microhabitat choice or competitive exclusion; see for examples in insects:

Peaterson & Mury 1979; Pyke 1982; Loreau 1989; birds: Schoener 1965, 1984; Dyamond 1975; mammals: Bowers & Brown 1982; Hopf, Valone & Brown 1993; Parra, Loreau & Jaeger 1999). Because fish show indeterminate and flexible growth, species and populations typically show a considerable variation in body size, where different-sized fish have sometimes been regarded as occupying different ecological niches (e.g. Birkett 1963). The size variations within ranks of *L. labiatus* were small, and the size range of a rank was separated from that of adjacent ranks except for the lowest ranks. We showed that in *L. labiatus* fish of the same ranks were strongly competitive (i.e. strongly aggressive with high resource overlapping) against each other, whereas fish between adjacent ranks were not, where niche differentiation induced from resource partitioning may be conceivable between the coinhabitants of adjacent ranks. Thus, from the viewpoint of feeding ecology, fish of different ranks can be regarded as 'different ecological species'.

We showed that the same- or similar-sized fish of *L. labiatus* showed territorial exclusion and fish from adjacent ranks accepted each other as coinhabitants despite regular aggressive interactions (dropping sharply in the large size difference). We showed that the body size ratios of adjacent ranks were 1.28 ± 0.07 SD ($n = 104$), which are determined non-randomly. As argued above, this value may be the best compromise between the individual's benefits of excluding a particular-sized competitor from the foraging territory and the costs of so doing. Although this 1.28 size ratio arises from the individual benefits and costs of within-species competition for resources, it is considerably similar to Hutchinson's rule, i.e. between-species body size ratios arising due to coinhabiting species competing for resources [Hutchinson 1959: size ratios (large/small) of approximately 1.3 (the exact ratio of 1.28 from samples listed in his Table 1)]. Moreover, body weight ratios (large/small) between closely related coinhabiting species are approximately 2.0 in some cases (e.g. Begon *et al.*, 1999: 1.28 is close to the cube root of 2.0). The mean weight ratio in adjacent rank fish of *L. labiatus* that shared the same home ranges was 1.99 ± 0.39 SD ($n = 36$). Arguably, both size ratios of the case of *L. labiatus* and of Hutchinson's rule should be deducible from the underlying individual-specific or species-specific preferences for resources and the costs and benefits of sharing these with other individuals or species depending on the body sizes of the competitors (Horn & May 1977; Roth 1981; Eadie, Broekhoven & Colgan 1987).

Empirical studies found evidence of communities apparently organized at least partly by differences in body size (e.g. Peaterson & Mury 1979; Pyke 1982; Schoener 1984; Dayan *et al.* 1989; Loreau 1989; Dayan & Simberloff 1994), although non-random size structure is not always shown (Begon *et al.* 1999). The general applicability of Hutchinson's rule, however, has been criticized, mainly because regularity in body size ratios have been found in some communities but not in others (e.g. Maiorana 1978; Simberloff & Boecklen 1981; Bowers & Brown 1982; Hopf *et al.* 1993; Parra *et al.* 1999). Some authors have suggested that when competition leads to Hutchinson's rule among coinhabiting species, some conditions should be

fulfilled: (1) densities of all the species considered should be limited by the same or similar resources (e.g. Maiorana 1978; Wiens & Rotenberry 1981). (2) Body size should have a direct and traceable effect on the resources preferred (Peaterson & Mury 1979; Wiens & Rotenberry 1981; Pyke 1982). (3) Species composition of a guild should be stable in evolutionary and current time-periods (Parra *et al.* 1999), i.e. not be due to random effects. (4) Coexistence mechanisms other than through resource partitioning should not play a major role (Roth 1981). (5) The presence of rare species should not affect the size structure strongly (Hopf *et al.* 1993; Parra *et al.* 1999). By default, our study system fulfills all these conditions extremely well. In contrast, these conditions rarely apply to across-species analyses in animal communities (e.g. Wiens & Rotenberry 1981; Begon *et al.* 1999), but communities probably fulfilling most conditions tend to appear to show regularity (e.g. Bowers & Brown 1982; Hopf *et al.* 1993; Parra *et al.* 1999).

As our study system consists of a single species of fish, each 'ecological species' (i.e. fish of the same ranks) will differ only in size but not in morphology and/or behavioural traits. In contrast, multiple species within ecological communities may evolve their general morphology, including body size, in response to a number of environmental factors (and sexual selection) other than competition (Wilson 1975; Eadie *et al.* 1987). Therefore, we argue that size regularity may be much more sharply detectable and deducible in *L. labiatus* communities (or communities of some other single fish species of group-living or with overlapping territories) than Hutchinson's rule (see also Hopf *et al.* 1993; Buston & Cant 2006). Nevertheless, we have argued above that similar ecological processes are expected to govern both size regularities of *L. labiatus* community and Hutchinson's rule. Understanding of body size ratios, for example, will enable us to predict the maximum number of overlapping territories or maximum number of coinhabitants (Hutchinson 1959; MacArthur & Levin 1967; Roth 1981; Buston & Cant 2006). Therefore, we propose that more examples are needed of size regularity of a single fish species of group living or with overlapping territories which may, at the same time, shed some light on Hutchinson's rule. If more examples are published and more experimental tests of the assumptions are performed, it will be particularly exciting to determine whether size regularity in these within-species fish communities is similar to Hutchinson's rule, and whether the underlying mechanism of competitive exclusion driven by body size-dependent resource preferences are sufficient to explain both.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Numbers of attacks, subordinate displays and ‘encounters’ observed in *Lobochilotes labiatus*.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2656.2008.1414.x>

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