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Differences in morphology and foraging behaviour in the goldcrest Regulus regulus and firecrest R. ignicapillus

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In a large area of sympatry, the goldcrest and the firecrest have overlapping territories. There is no evidence of interspecific territoriality or dominance by one species over the other. A close investigation of foraging behaviour, including choice of habitat, foraging postures and feeding curves, and of morphology (58 external and skeletal features measured) showed that their co-existence is facilitated by differences in feeding ecology. In a large outdoor aviary, newly caught birds were confronted with experimental trees denuded of natural food and their movements and postures were recorded. Independent of kind and occurence of prey, there are specific differences in preference for deciduous and coniferous trees and in the mode and speed of foraging. Firecrests show no particular preference between spruce and beech, whereas goldcrests clearly prefer spruce. Firecrests move more rapidly. Firecrests forage more often standing, whereas goldcrests more often cling vertically and hang. Differences in behaviour are more pronounced than differences in morphology investigated by multiple discriminant function analysis, but there are some morphological correlates: length of rictal bristles, width of gape and length of hind claw. External morphological characters discriminated best, then skeletal features and finally features of the flight apparatus. Furthermore, there are differences in the structures of the soles of the feet. Goldcrest soles are provided with deep furrows capable of gripping individual needles; firecrests have a smoother surface.

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1. Introduction

Recent studies have clarified some of the problems of co-existence between the goldcrest (GC, *Regulus regulus*) and the firecrest (FC, *R. ignicapillus*). Becker (1977a, b) and Thaler (1979) have both recently investigated ethological isolating mechanisms between the two species. In addition, Thaler & Thaler (in press) also investigated prey selection. However, several important questions still remain with regard to the co-existence of these two species. For example several authors (Voous 1962, Lack 1971, Mauersberger & Stübs 1971) have claimed that there are interspecific differences in habitat requirements, whereas our observations suggested that these species frequently have overlapping territories, and Becker (1977b) did not find any differences in the main habitat requirements. We also found no evidence of interspecific territoriality or dominance by one species over the other.

We therefore decided to investigate several aspects of habitat requirements, foraging behaviour and morphology in order to elucidate the interspecific relations between the two species.

2. Material and methods

The difficulties of observing such small birds high in the canopy were avoided by studying the following aspects of behaviour on captive wild birds: 1) choice of foraging habitat, 2) foraging postures, 3) feeding curves. In addition, we investigated external morphology and some skeletal features. One advantage of simultaneously carrying out morphological work and eco-ethological observations in an integrated study is that it leads to permanent feedback between laboratory and field investigations during the whole study (Bock 1974, Leisler 1980a).

Three different kinds of tests were done in a large (10 x 5 x 3 m) outdoor aviary during October/November. A total of 23 recently caught birds (13 goldcrests, 10 firecrests) were used in the experiments. The birds were initially housed in a smaller aviary for some weeks before testing. Food was provided ad libitum in both aviaries, but because of the normally high feeding rate in such small birds this did not influence normal foraging behaviour. The experimental trees in the aviary were denuded of natural food by regular high pressure spraying with water. The differences in foraging behaviour found were thus unbiased by differences in food availability, different prey distribution and food types, which might otherwise confuse the interpretation of field data. It was impossible to test a single bird as it immediately tried to communicate with a non-captive conspecific. Birds were therefore held in the test aviary in conspecific pairs, but only one bird was tested. After a 40 min recording a new pair was introduced to avoid bias from a possible tradition developed by the birds in the aviary. The testing scheme was as follows: AB, A tested, CD, D tested, BF,

Table 1. Morphological characters used in discriminant function analyses.

External characters	Skeletal characters	Flight apparatus
1 Wing length	1 Coracoid length	1 Alula
2 Tail length	2 Height of crista sterni	2 Primary X
3 Tarsus	3 Pelvis length	3 Primary IX
4 Bill length/skull	4 Pelvis width	4 Primary VIII
5 Bill depth	5 Sternum length	5 Primary VII
6 Bill width/nostril	6 Sternum width	6 Primary VI
7 Bill width/base	7 Femur	7 Primary V
8 Hind toe	8 Tibiotarsus	8 Secondary 1
9 Inner toe	9 Tarsometatarsus	9 Secondary 2
10 Middle toe	10 Humerus	10 Notch of primary VIII
11 Outer Toe	11 Ulna	11 Notch of primary VII
12 Hind claw	12 Metacarpus	12 Notch of primary VI
13 Inner claw	13 Interorbital width	13 Notch of primary V
14 Middle claw	14 Premaxilla length	14 Longest rectrix
15 Outer claw	15 Premaxilla width	15 Shortest rectrix
16 Foot span	16 Mandible length	16 Wing tip to primary X
17 Foot span with claws	17 Mandible width	17 Wing tip to secondary 1
18 Rictal bristles	18 Postorbital width	18 Graduation of tail
19 Wing tip to secondary 1		
20 Wing span		
21 Wing area		
22 Chord of wing		

B tested, etc. Further observational methods will be discussed in connection with the results.

We measured 58 different morphological characters belonging to three complexes: 22 external characters (GC n = 23, FC $n = 20$), 18 skeletal and 18 flight characters (GC $n = 36$, FC n = 23) (see Table 1). The data fall into two groups: adult males and a more heterogeneous group which included females and immature birds.

3. Results

3.1. Behaviour

Choice between beech and spruce

A small spruce and a small beech tree were placed in the aviary during the test. The total observation time was 40 min for each bird, the position of the trees being reversed after 20 min. Figure 1 shows the percentage of time spent by 11 goldcrests and firecrests in each tree and the number of times the birds entered the two trees. The species differ significantly in their use of the two trees ($P < 0.001$ in both tests, Kolmogorov-Smirnov test). In both cases goldcrests showed a significant preference for spruce, whereas firecrests showed no particular preference.

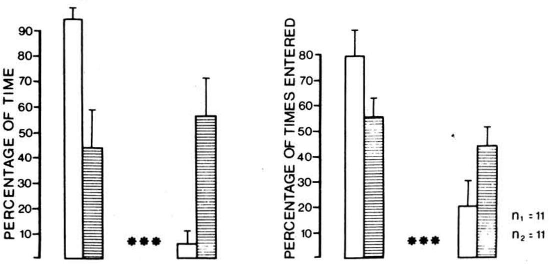

Fig. 1. Percentage of time spent by 11 goldcrests (white column) and 11 firecrests (hatched column) in a spruce (S) and beech (B) tree (left-hand side); percentage of times the birds entered the two trees (right-hand side).

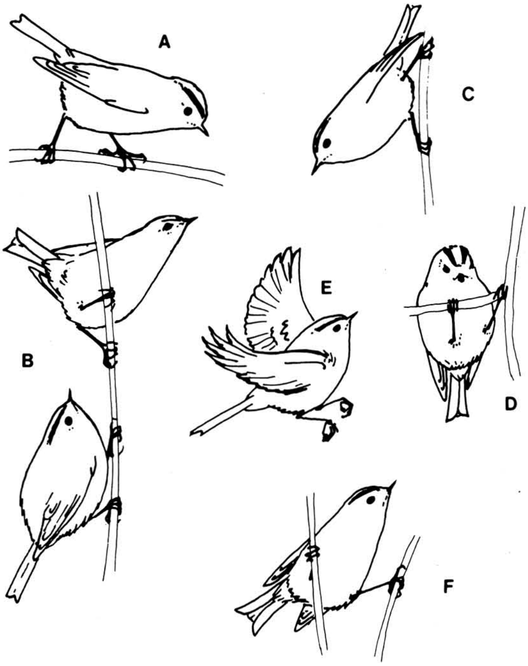

Fig. 2. Foraging postures recorded: A standing, B clinging vertically head up, C hanging vertically head down, D hanging horizontally, E hovering, F double grip position.

Foraging postures on different branches

Postures were recorded in the following six categories (similar to Partridge 1976) shown in Fig. 2: A) standing (centre of gravity above feet), B) clinging vertically head up (centre of gravity level with the feet), C) hanging vertically head down, D) hanging horizontally (centre of gravity below feet), E) hovering, F) double grip position. These postures were recorded on 14 different branches (9 spruce, 2 pine, 3 oak).

Figure 3 shows the differences in the percentages of different postures adopted by the birds (9 firecrests, 9 goldcrests) during the experiment. Firecrests showed significantly more standing ($P < 0.001$), whereas goldcrests showed significantly more vertical clinging and hanging,

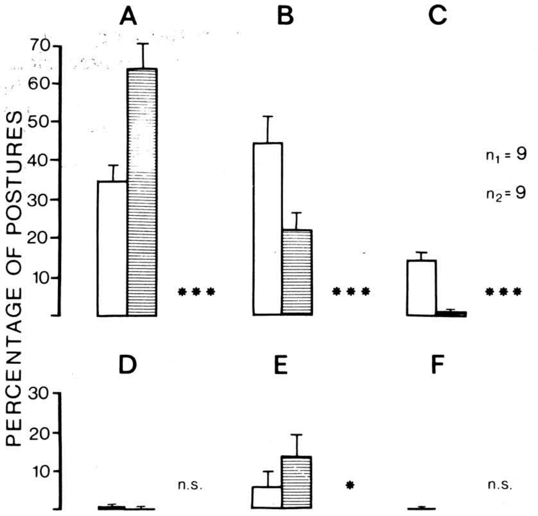

Fig. 3. Percentage of postures A -F adopted by 9 goldcrests (white column) and 9 firecrests (hatched column).

both head up and head down ($P < 0.001$, Kolmogorov-Smirnov-test). Firecrests also hovered significantly more ($P < 0.05$).

These differences might be due to preferences for particular branches and so we examined the results for each branch. In the case of branch No. 5 (a spruce with hanging, comb-like twigs), both species frequented it at the same rate (goldcrest $\bar{x}$ 28.28 ± 8.73 % of times entered, firecrest $\bar{x}$ 28.91 ± 9.23 %). The overall pattern of postures remained the same as before.

Next we investigated branch No. 9 (on which the needles were evenly distributed), which the species visited at different frequencies (goldcrest $\bar{x}$ 0.44 ± 4.26 %, firecrest $\bar{x}$ 5.77 ± 2.67 %). The difference in posture A then disappears, because both species are forced to stand and feed on this kind of branch structure. The other differences remain at a similar level.

Feeding curves

To test for differences in foraging behaviour, 14 trees (10 spruce, 2 pine, 1 beech, 1 oak) were placed in the outdoor aviary to form a small wood. We recorded the total distance each bird travelled while foraging, the number of stops made, and the amount of time spent stationary.

From (1) the average speed of progression, (2) number of stops, and (3) mean duration of stops we constructed a 'sawtooth' curve (Cody 1968, 1974). Goldcrests move more slowly than firecrests and so the curves for the two species do not even overlap, despite considerable intraspecific variation (Fig. 4).

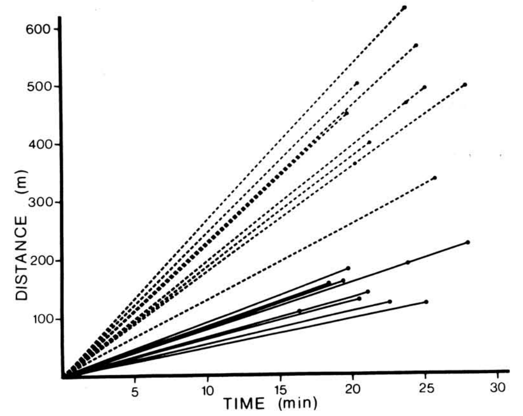

Fig. 4. Speed of progression of 10 firecrests (broken lines) and 10 goldcrests (solid lines).

Table 2 gives quantitative data of the species' foraging behaviour from averaged steps in the feeding sequences. The only significant difference is in the speed of progression from one tree to the next, not in the number of stops or in the time spent stationary. In this situation we also obtained information regarding preferences for particular trees. Again beech was frequented more by firecrests ($\bar{x}$ 13.9 ± 8.6 % of times entered) than by goldcrests ($\bar{x}$ 2.2 ± 7.0 %, $P < 0.05$, Kolmogorov-Smirnov test).

3.2. Morphology

Body size

First we investigated whether there were any differences in size between the two species. Thaler & Thaler (in press) found that there were no significant differences in mean body weight during the breeding season: both species weigh 5.1 g. As body weight is affected by various seasonal and age-dependent changes we calculated

Table 2. Averages (± SD) for four variables describing the movements of goldcrest and firecrest in the experiments. $n = 10$.

	Goldcrest	Firecr	
Number of stops	40.4±10.9	38.2±1[illegible]	n.s
Time spent stationary (sec.)	222.0±52.53	192.4±72.57	n.s
Duration of stops (sec.)	5.68±1.51	5.13 ±1.79	n.s
Distance (cm)	19.5±4.6	66.5±13.3	$P < 0.001$

Table 3. Most important external characters for discriminating between the two species (correlation coefficients with discriminant axis I). Figures in parentheses refer to the character number listed in Table 1. Right-hand part of the table gives the character means of adult males and P values for univariate comparison. $n = 16$.

Character	Corr.	Goldcrest	Firecrest	P
Rictal bristles (18)	0.770	6.06±0.52	6.88±0.52	< 0.001
Hind claw (12)	-0.723	5.61±0.19	5.11±0.23	< 0.001
Outer toe (11)	0.495	6.25±0.24	6.44±0.23	< 0.05
Middle claw (14)	0.477	4.16±0.17	3.94±0.19	< 0.01
Middle toe (10)	0.456	8.21±0.33	8.49±0.39	< 0.05
Bill width/nostril (6)	0.422	2.55+0.14	2.67±0.17	< 0.05

'body size' from different skeletal features. 'Body size' = (sternum length + pelvis length + coracoid length) x (sternum width + pelvis width) x (height of crista sterni) (Hoerschelmann 1966, Stork 1968, Rüger 1972, Leisler 1980b). There was no significant difference between 'body size' in the goldcrest ($n = 18$ adult males, $\bar{x}$ 1271.31 ± 63.12) and the firecrest ($n = 15$ adult males, $\bar{x}$ 1280.24 ± 72.78, t-test). Therefore, there is no need to scale the data according to body size.

External characters

Data were analyzed by multiple discriminant function analysis to find which characters best discriminate between the four groups (goldcrest adult males, goldcrest others, firecrest adult males, firecrest others).

Table 3 ranks the characters investigated in order to show which are the most important in discriminating between the two species (correlation coefficients). Also shown are the means of adult males and the significance levels for univariate comparisons. The biggest difference between the two species is in the length of the rictal bristles. The firecrests use longer rictal bristles for feeding on larger moving prey. The functional significance of rictal bristles has only recently been shown by Conover & Miller (1980). They protect a bird's eye from food items the bird is trying to capture and might have an important function in manipulating and directing food into the gape (Lederer 1972). The next best character is the length of digit I (hind toe). Goldcrest use their longer D I for vertical clinging (for the functional significance, see Rüggeberg 1960). The next best character is length of the outer and middle toes, which in the firecrest form a foot somewhat better adapted for perching on branches. A multiple discriminant function analysis of the four groups separates both species with no overlap (Fig. 5).

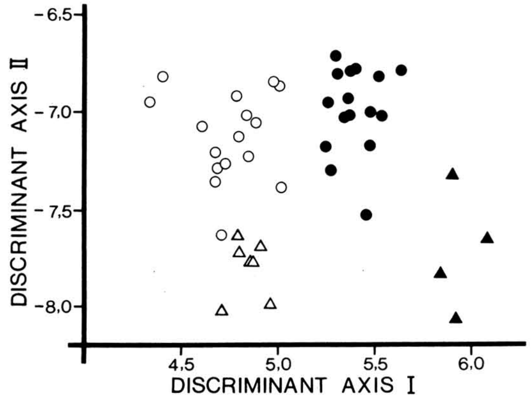

Fig. 5. Separation of goldcrest (open symbols) and firecrest (solid symbols) as shown by discriminant function analysis of 22 external characters. Circles: adult males, triangles: others.

Skeletal characters

The biggest difference between the species is in the width of the premaxilla (Table 4). Firecrests have a broader bill than goldcrests, which feed on smaller prey items (Thaler & Thaler, in press) and probe more frequently between the needles. The next most important feature is pelvis width, which remains difficult to interpret. Further studies on the areas of origins and aponeuroses of pelvic muscles are needed. The next difference is in humerus length, where firecrests may use their longer humerus for making longer and more sustained flights. A multiple discriminant analysis yields quite a good separation of the two species (Fig. 6).

Flight apparatus

Table 5 ranks the characters of the functional complex for flight according to their discriminant value. The length of primary IX is the best discriminator. The firecrest has a somewhat shorter primary IX than the goldcrest, forming a more rounded wing tip. The next best character is length of the alula, goldcrests having somewhat longer alulae. A substantial alula functions as a producer of high lift at very high angles of attack and is used by birds in slow flight and for stopping

Table 4. Most important skeletal characters for discriminating between the two species (correlation coefficients with discriminant axis I). For further explanations see Table 3.

Character	Corr.	Goldcrest ($n = 18$)	Firecrest ($n = 15$)	P
Bill width (15)	-0.817	3.11±0.16	3.47±0.18	< 0.001
Pelvis width (4)	0.682	6.83±0.16	6.63±0.20	< 0.01
Humerus (10)	-0.484	9.44±0.17	9.69±0.18	< 0.001

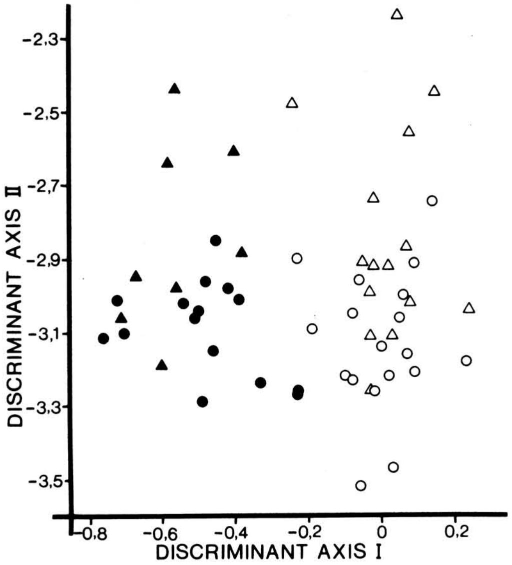

Fig. 6. Separation of firecrest and goldcrest as shown by discriminant function analysis of 18 skeletal characters. Symbols as in Fig. 5.

their flight (Nachtigall & Kempf 1971). This corresponds with the goldcrest's slower progression speed in shorter steps.

The next character is graduation of the tail. The tail of the goldcrest is as long but more forked than that of the firecrest. This difference might be related to different modes of hovering in the two species: goldcrests display very short stops in the air, hovering in front of twig tips, whereas firecrests hover switching from one twig to another. Fig. 7 shows that features of the flight apparatus separate the species least.

We found striking differences in the structure of the soles of feet between the two species. Pads, papillae and folds on the sole form a set of features which are adapted to the substrate by increasing friction and surefootedness (Rüggeberg 1960, Lennerstedt 1974).

Table 5. Most important characters of the flight apparatus for discriminating between the two species (correlation coefficients with discriminant axis I). For further explanations see Table 3.

Character	Corr.	Goldcrest (n = 19)	Firecrest (n = 16)	P
Primary IX (3)	0.732	39.76±0.91	38.19±0.99	< 0.001
Alula (1)	0.634	13.89±0.71	13.16±0.60	< 0.01
Graduation of tail (18)	0.523	3.87±0.92	2.98±0.72	< 0.01
Notch of primary VII (11)	-0.333	16.96±1.04	17.43±0.82	n.s

Figure 8 shows a lateral view (left) of the foot of the two species. In the goldcrests the papillae of the pads of digit IV (outer toe) form protruding tubercles and the pads are separated by deep furrows which are capable of gripping around individual needles. The medial view (right) shows that deep furrows are widely distributed on all toes of the goldcrest, whereas the pads form a smoother surface in the firecrest.

4. Discussion

Our results suggest that the goldcrest is morphologically and behaviourally more specialized to foraging in coniferous trees. The firecrest appears to be less specialized. The preference of goldcrests for coniferous woodland, however, has been questioned by several workers (summarized in Becker 1977b). The species differ particularly in foraging speed and postures, which means that branches are exploited in different ways. Field observations by Thaler & Thaler (in press) corroborate our finding that the use of the wing plays a more important role in habitat utilization in the firecrest than in the goldcrest. The longer distances of travel observed in the firecrest are in concordance with predictions of an optimum foraging theory concerning optimum distance between feeding sites, prey detectability and density. Andersson (1981) predicted that the distance moved by a predator should increase

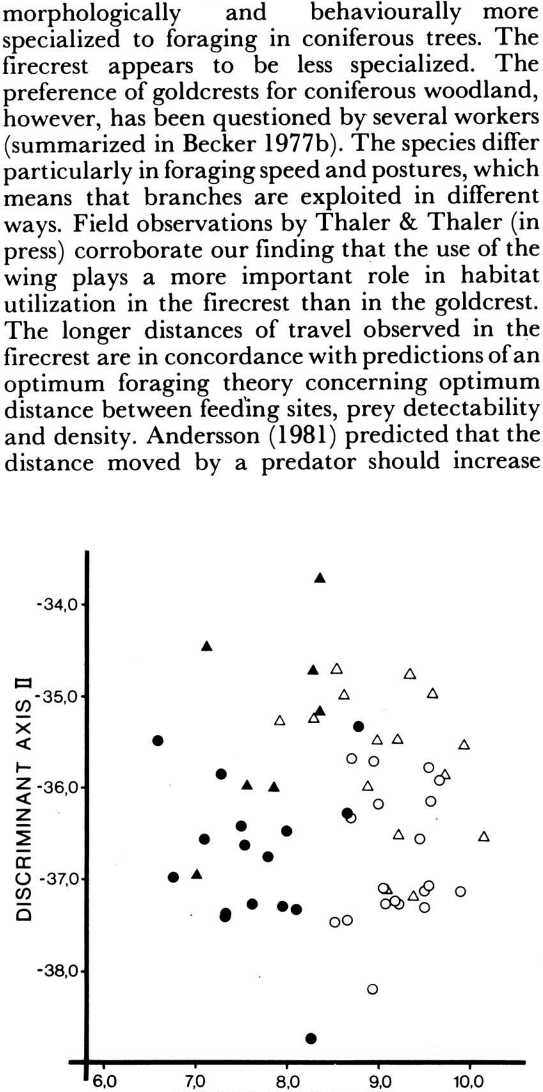

Fig. 7. Separation of goldcrest and firecrest as shown by discriminant function analysis of 18 characters of the flight apparatus. Symbols as in Fig. 5.

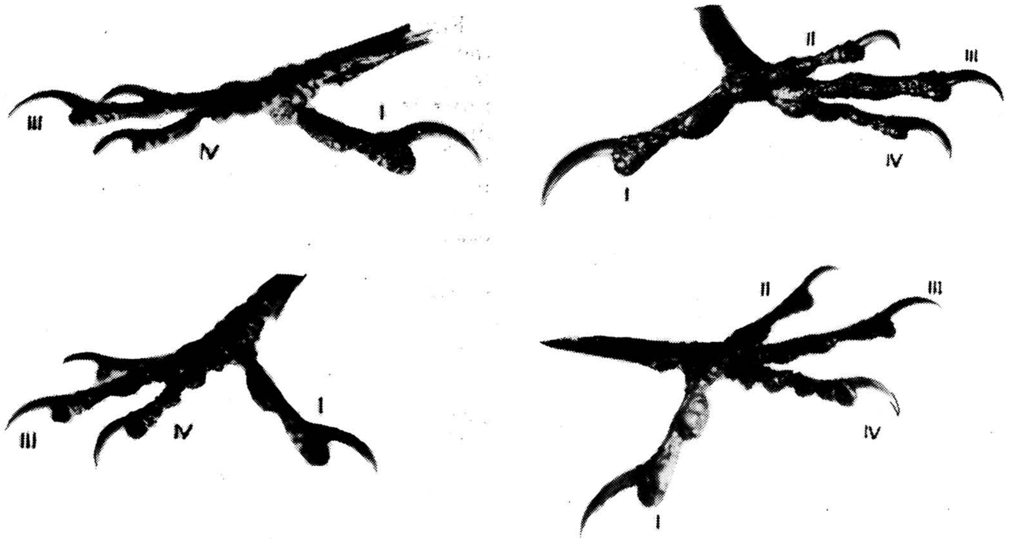

Fig. 8. Feet of firecrest (top) and goldcrest (bottom) in lateral (left) and medial (right) view. I hind toe, II inner toe, III middle toe, IV outer toe.

with more easily detectable prey, which in our case means larger size (firecrests feed on larger prey than goldcrests). Although Andersson's model is derived for predators hunting in twodimensional habitats, the qualitative conclusions should also apply to predators hunting in three-dimensional space, such as our birds. Our findings on the frequency of hovering may have been biased as goldcrests only hover for very short periods, whereas firecrests hover in a much more obvious and sustained manner, which may cause an underestimation of hovering flights in the goldcrest.

It seems interesting to assess the degree of divergence in behaviour and morphology of the two species. For this we compare results of the ethological experiments with results of the discriminant analyses of morphological traits. It becomes clear that we found differences without overlap between the two species in several aspects of foraging behaviour, whereas discriminant analyses (which push the species apart) achieve a complete separation in only one case. Thus as a whole, differences in foraging behaviour are much more pronounced than differences in morphology, but some morphological correlates of behavioural differences were found (rictal bristles, width of gape, hind claw). The best morphological characters are external features, then skeletal features and finally features of the flight apparatus. The firecrest (distributed in the southwest of Europe) and the goldcrest (with a more northeasterly distribution) apparently evolved from a common ancestor (Steinbacher 1927, Salomonsen 1931, Löhrl & Thaler 1980), but did so in different refuges dominated by differing floras and food regimes. In our opinion, the existing broad differences in habitat utilization developed in allopatry and thus there is no need to invoke competition in the current areas of sympatry to explain the ecological differences between the two species.

What general conclusions can be drawn from our investigation? Studies on co-existence between closely related species usually find some differences in foraging ecology (see Morse 1980 for reviews). Therefore, our findings are not altogether surprising. However, in an increasing number of studies there are deductions from relatively few morphological data in order to assess the similarity or dissimilarity of species. For example, bill length has often been used to calculate character ratios between species (Hutchinson 1959, Schoener 1965). Ecologically similar species should differ in bill size or body size by some relatively constant proportion (1 : 1.3.) in order to coexist (see Wiens this issue, and Lederer, in press, for critical reviews). Another generally accepted hypothesis is that differences in bill size are closely related to differences in size of prey captured (Grant 1965, 1967, 1968; Hespenheide 1973, Beaver & Baldwin 1975, Abbott 1977, Herrera 1978, Smith & Zach 1979, see also Lederer, in press, and Wiens & Rotenberry 1980, for critical reviews). With the assumption that bill length is related to prey size, it has often been inferred that species are not separated in feeding ecology. However, species pairs with the same bill length (character ratio 1.00), such as the goldcrest and firecrest, can show significant differences in foraging behaviour. According to Hulsman (1981), in some terns the width of the gape is more closely related to the size of the prey than bill length.

Our study shows that many more morphological measurements must be taken, such as width of gape and length of rictal bristles, together with eco-ethological observations and experiments to assess accurately the similarity or dissimilarity of species pairs.

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