

ECOMORPHOLOGY OF THE NORTH AMERICAN RUBY-CROWNED (*REGULUS CALENDULA*) AND GOLDEN-CROWNED (*R. SATRAPA*) KINGLETS

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ABSTRACT.—We analyzed body morphology relative to habitat utilization and locomotory feeding movements in the Ruby-crowned (*Regulus calendula*) and Golden-crowned (*R. satrapa*) kinglets. The Ruby-crowned Kinglet has a relatively longer, wider, and shallower bill, longer rictal bristles, and a longer humerus and ulna. The capture of aerial prey and the plucking of insects from foliage, which require somewhat complicated aerial maneuvers, made up 24 and 27% of the Ruby-crowned Kinglet's locomotory feeding movements; and they made up 2 and 13% of the Golden-crowned Kinglet's feeding movements. The Golden-crowned Kinglet has relatively shorter tarsi and longer toes than the Ruby-crowned, and highly grooved soles of the feet. Golden-crowned Kinglets hung or clung from foliage in 43% of prey attacks, whereas the Ruby-crowned Kinglet hang-gleaned in only 7%. The Golden-crowned Kinglet fed predominantly in conifers, the Ruby-crowned in deciduous trees.

In some major patterns of divergence and specialization, the two North American species are comparable to those found by Leisler and Thaler (1982) for the Palearctic *R. regulus* and *R. ignicapillus*. Received 17 April 1990, accepted 1 April 1991.

THE GENUS *Regulus*, a group of small-bodied insectivorous warblers, comprises two pairs of species; one pair occurs in the northern forests of the Nearctic and the other in the Palearctic forest. Leisler and Thaler (1982), in an innovative study involving quantification of morphological characters, feeding patterns, and habitat utilization patterns, compared the Palearctic Goldcrest (*R. regulus*) and Firecrest (*R. ignicapillus*). Differences were found in bill width, length of rictal bristles, length of humerus, shape of wing and tail, length of alula, and morphology of the soles of the feet. These features reflected differences in foraging and habitat-use patterns.

We made a comparative study of the two North American species, the Ruby-crowned Kinglet (*Regulus calendula*) and the Golden-crowned Kinglet (*R. satrapa*). We analyzed the morphology of each species and related differences to locomotory feeding movements and substrate utilization patterns.

METHODS

Morphometric measurements.—We measured 8 skeletons and 10 museum skins of males of each species as follows: (1) *Skeleton*—we measured total length of fused vertebral column (thoracic, lumbar, and sacral vertebrae combined); length of cervical vertebrae; total skull length; maximum skull width and depth; bill length, frontal-nasal hinge to tip; width and depth

of the bill at the skull; length and width of mandible; sternum length and width; lengths of femur, tibiotarsus, tarsometatarsus, and middle toe (foot digit 3) without claw; lengths of humerus, ulna, carpometacarpus, hand digit 3 (phalanx 1 and phalanx 1+2). (2) *External morphology* (from museum skins)—bill length, tip to rear of nares; bill width and depth at rear of nares; length of rictal bristles; lengths of wing chord, tail, centralmost and outermost rectrices, tarsometatarsus, middle toe (digit 3) without claw, middle toe claw, hallux without claw, hallux claw, footspan with claw; lengths of alula, primaries 10–5, and secondaries 1 and 2. Because the skeletons and skins necessarily represented different individuals, the two data sets are treated independently and some measurements were repeated for each series. Body weight, wing aspect ratio (ratio of length to breadth of wing), and wing loading (mass per unit area of wing; $\text{g}\cdot\text{cm}^{-2}$) were obtained from live birds trapped during northward migration at Prince Edward Point, Ontario. Drawings of the feet of these birds were made. Some of the measurements are not independent and overlap (see also Leisler and Thaler 1982). Examples are the bill measurements, and "footspan with claws" relative to "hind toe length," and "hind claw length." Footspan is an adaptive complex reflecting the individual's ability to perch on substrates of different diameters; hind toe length reflects its ability to cling from vertical surfaces. The units of the foot are potentially adaptive individually and as a member of a complex. The additional measurements are included on this basis.

Morphological variables were grouped into functional units related to specific biological functions,

following Oxnard (1973, 1975), and Leisler and Winkler (1985). The morphological data were analyzed with factor analysis to resolve differences between species, supplementing absolute measurements. Results presented for factor analyses are factor correlations (loadings) for orthogonally rotated variac solutions, to best suit the data, using Macintosh StatView SE-Graphics, V.1.02. We were interested in analyzing groups of characters related to specific biological functions logically or through previous studies in the literature so that any relative differences in these could be compared directly with the ecological data we have a reason to think should be related.

Factor 1 was designated as an overall approximation of size variation within the functional complex (which is generally true) when (1) all loadings on that factor were in the same direction corresponding to a joint increase (or decrease) in all measures, (2) the coefficients were of similar magnitude, and (3) the factor represented a large proportion of the variance in the data. When these three conditions were met, the subsequent factors were interpreted as axes of shape variation within the functional complex (see Mosimann and James 1979, Bookstein et al. 1985, Grant 1986). When these criteria were not met, the essence of a factor representing "size" in that complex of characters is noted.

Locomotory feeding movements and substrate utilization.—Data were obtained in southeastern Ontario at Little Cataraqui Creek, near Kingston, and Prince Edward Point, near Picton, between 15 April and 10 May, 1989. The sites contained a diversity of both conifer and deciduous (bare and newly leafed) trees and shrubs, which permitted the species to express any feeding substrate and habitat-use preferences. Data on percentages of foraging individuals that fed in coniferous and deciduous trees, foraging tactics, and locomotory feeding movements were quantified by the methods of Robinson and Holmes (1982) and Holmes and Recher (1986). The major problems associated with these types of data are biases introduced by the interrelatedness of sequential feeding movements, inadequate spreading of observations over time, and small sample sizes (Petit et al. 1990). We reduced these problems by standardizing data-gathering to 20–40 s per bird, monitoring each individual or feeding party only once, sampling both the morning and evening feeding periods, and extending data collection throughout the entire 4–5-week period.

RESULTS

Morphology.—The analyses were conducted separately for each of six functional units as follows.

(A) *Axis of leg, skeletal* (femur, tibiotarsus, tarsometatarsus, and middle toe [digit 3] without claw). Femur, tibiotarsus, and tarsometatarsus

load strongly and relatively evenly on factor 1 (Table 1A). Femur, tibia, and tarsus function as a group and appear to represent a size-of-leg factor which separates the two species. The Ruby-crowned Kinglet has the longer leg (Fig. 1A). The middle toe (digit 3) does not appear to be associated with the other three variables. Factor 2 explains 99% of the variance in digit 3 but does not clearly separate the kinglet species.

(B) *Leg and foot dimensions, museum skins* (tarsometatarsus, middle toe [digit 3], middle claw, hind toe [hallux], hind claw, footspan with claw). The two species separate along a factor of tarsus relative to hind toe and hind claw (Tables 2 and 1B, Fig. 1B). The Ruby-crowned Kinglet has relatively longer tarsi and shorter hind toes and hind claws. Factor 2 loads strongly for footspan with claw and does not separate the species.

(C) *Wing axis, skeletal* (humerus, ulna, carpo-metacarpus, phalanx 1, phalanx 1+2). The species are separated along factor 1 or "size of wing," which loads positively for all elements (Table 1C, Fig. 1C). Factor 2, interpreted as distal relative to proximal elements of wing, also separates the two species but to a lesser extent than factor 1. There is a trend towards longer distal relative to proximal elements in the Golden-crowned Kinglet.

(D) *Flight features, museum skins* (alula, primaries 10–5, secondaries 1 and 2, tail length, tail fork depth). There does not appear to be a general size factor relating these variables. Factor 1 is most highly correlated with the major primaries, 8–5, and tail length (i.e. with length of wing and tail as determined through feather length; Table 1D). The two species do not appear to separate on this axis; both have an almost equal distribution (Fig. 1D). Factor 2, a measure of width of wing and tail shape, is highly positively correlated with secondaries 1 and 2, and strongly negatively correlated with tail fork depth (and with the vestigial primary 10). The species do not overlap along this axis. The Golden-crowned Kinglet has a relatively deeper tail fork and shorter secondaries than the Ruby-crowned Kinglet.

(E) *Body long axis, skeletal* (fused vertebral column [i.e. thoracic, lumbar, and sacral vertebrae], length of cervical vertebrae [total], skull length without bill, bill length). Factor 1 is defined by the thoracic vertebrae, cervical vertebrae, and skull (Table 1E). Bill length loads in the same direction but to a lesser extent. Factor 2 is highly

TABLE 1. Correlations (loadings) of morphological variables measured for Ruby-crowned and Golden-crowned kinglets with orthogonally rotated multivariate factors. (A) Axis of leg, skeletal; (B) leg and foot dimensions, museum skins; (C) wing axis, skeletal; (D) flight features, museum skins; (E) body long axis, skeletal; and (F) bill morphology, museum skins.

Variable	Correlations with orthogonal factors (F)		Variable	Correlations with orthogonal factors (F)	
	F-1	F-2		F-1	F-2
(A) Axis of leg, skeletal			(D) Flight features, museum skins		
Femur length	0.923	0.234	Alula	0.076	-0.229
Tibiotarsus length	0.958	0.112	Primary 10	0.369	-0.643
Tarsometatarsus length	0.966	-0.018	Primary 9	0.274	0.045
Mid. toe (digit 3) length	0.101	0.993	Primary 8	0.804	-0.276
% prop. variance explained	72.1	27.9	Primary 7	0.793	0.213
			Primary 6	0.841	0.123
			Primary 5	0.844	0.102
			Secondary 1	0.303	0.906
			Secondary 2	0.234	0.938
			Tail length	0.740	-0.124
			Tail fork depth	0.171	-0.918
			% prop. variance explained	43.4	37.9
(B) Leg and foot dimensions, museum skins			(E) Body long axis, skeletal		
Tarsometatarsus length	-0.851	-0.144	Bill length	0.29	0.950
Mid. toe (digit 3) length	-0.046	-0.038	Skull length	0.927	0.166
Mid. toe (digit 3) claw length	-0.284	-0.011	Cervical vertebrae	0.866	0.402
Hind toe (hallux) length	0.687	-0.230	Thoracic, lumbar, & sacral vertebrae	0.851	0.437
Hind toe (hallux) claw length	0.882	0.044	% prop. variance explained	65.3	34.7
Foot span	-0.455	0.738			
Foot span with claw	0.227	0.900			
% prop. variance explained	39.9	24.7			
(C) Wing axis, skeletal			(F) Bill morphology, museum skins		
Humerus length	0.903	-0.290	Bill length	0.701	-0.637
Ulna length	0.858	-0.350	Bill width	0.949	-0.251
Carpometacarpus length	0.691	0.654	Bill depth	-0.270	0.949
Phalanx 1 (of major digit)	0.892	0.104	% prop. variance explained	51.7	48.3
Phalanx 1 + 2 (of major digit)	0.815	0.022			
% prop. variance explained	84.4	15.6			

correlated with bill length. Both factors separate the species (Mann Whitney U-test, $P < 0.05$; Fig 1E). The Ruby-crowned Kinglet has a longer bill and longer body axis.

(F) *Bill morphology, museum skins* (total length to back of nares, width and depth at back of nares). Both bill width relative to length (factor 1) and depth relative to length (factor 2) clearly separate the kinglets (see also Table 2). Bill length and width load strongly and positively on factor 1. Bill depth loads negatively and more weakly. Factor 2 is correlated strongly and negatively with bill length, but positively with bill depth (Table 1F). The Golden-crowned Kinglet has a shorter, narrower, and deeper bill.

Factor analyses (and univariate comparisons;

Table 2 and below) show that the Ruby-crowned Kinglet has a longer leg; the Golden-crowned Kinglet has relatively longer hind toes and hind claws. The Golden-crowned Kinglet has shorter skeletal wing elements, particularly humerus and ulna. The Golden-crowned Kinglet has relatively shorter secondaries and a relatively deeper tail fork than the Ruby-crowned. The bill is shorter, narrower, and deeper than that of the Ruby-crowned Kinglet. Three of the major differences between the kinglet species are in the distal members of linear series: the tarsometatarsus and toe within the leg, distal skeletal wing elements (carpometacarpus, phalanx 1, phalanx 1+2) relative to the humerus and ulna, bill length along the main body axis.

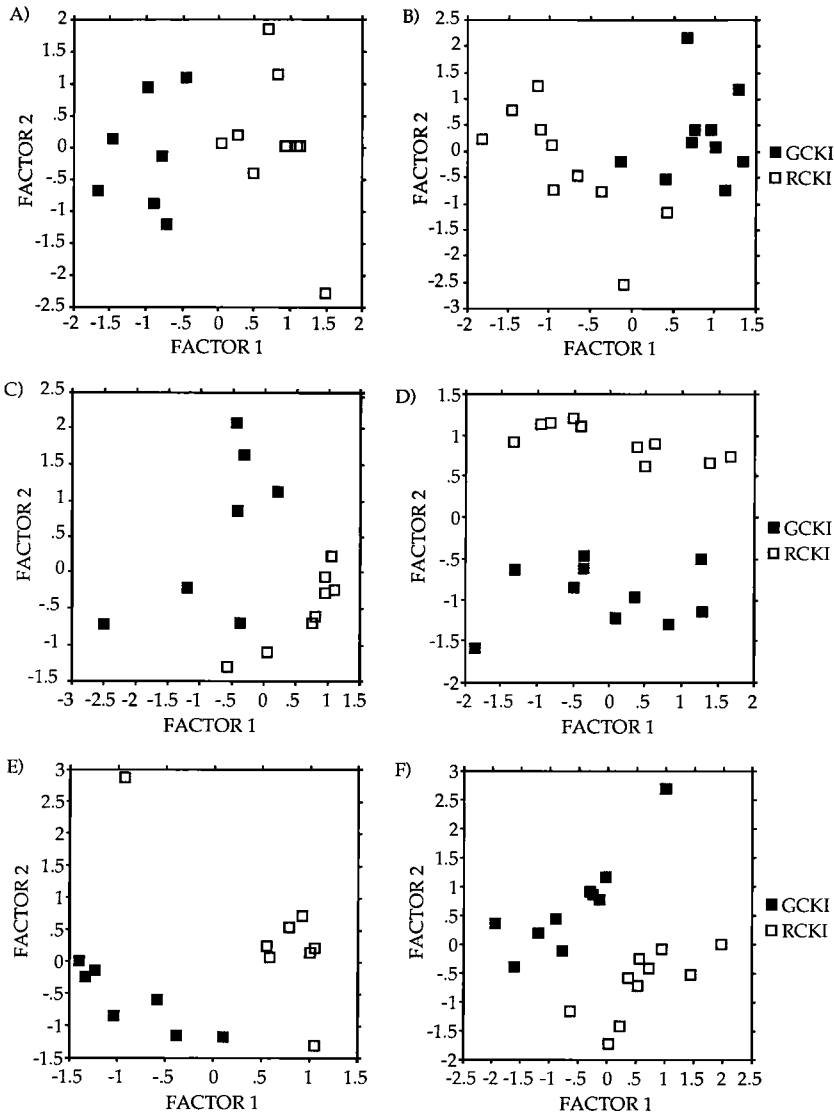


Fig. 1. Factor 1 vs. Factor 2 from factor analysis of groups of morphological variables measured in the Ruby-crowned (RCKI) and Golden-crowned (GCKI) kinglets (for details see text). (A) Axis of leg, skeletal; (B) Leg and foot dimensions, museum skins; (C) Wing axis, skeletal; (D) Flight features, museum skins; (E) Body long axis, skeletal; and (F) Bill morphology, museum skins.

In the Ruby-crowned Kinglet, bill length, bill width, rectal bristle length, and tarsus length are significantly greater ($P < 0.0001$), and the body is significantly heavier ($P = 0.01$) than the Golden-crowned (Table 2). The bill of the Ruby-crowned Kinglet is significantly shallower ($P < 0.0001$). The hallux length without claw of the Golden-crowned Kinglet is significantly longer ($P = 0.0360$). Wing chord and tail length are not significantly different. Aspect ratio of

the wing, and wing loading, appear similar in the two species.

The species differ strikingly in the structure of the underside of the toes and soles of the feet. In the Ruby-crowned Kinglet these areas are relatively smooth, but in the Golden-crowned Kinglet the papillae of the pads are exaggerated to form protruding tubercles separated by deep furrows (Fig. 2). The scales are also larger in the Golden-crowned.

TABLE 2. External morphological features of Ruby-crowned and Golden-crowned kinglets, based on museum skins ($\bar{x} \pm SD$) and live birds (\bar{x} [range]). The measurements are based on series of 10 adult male Ruby-crowned Kinglets and 20 adult male Golden-crowned Kinglets. Significance (*) was determined by two-tailed unpaired *t*-tests.

Measurement	Ruby-crowned Kinglet	Golden-crowned Kinglet	<i>P</i>
Museum skin			
Wing chord length (mm)	58.6 \pm 1.51	58.0 \pm 1.33	0.3599
Tail length (mm)	43.6 \pm 0.40	43.7 \pm 0.47	0.8735
Bill length (mm)	8.35 \pm 0.08	6.55 \pm 0.10	0.0001*
Bill width (behind nostril) (mm)	3.55 \pm 0.06	3.17 \pm 0.06	0.0002*
Bill depth (mm)	2.17 \pm 0.04	2.63 \pm 0.06	0.0001*
Rictal bristle length (mm)	4.2 \pm 0.41	3.7 \pm 0.31	0.0001*
Tarsus length (mm)	17.52 \pm 0.45	15.35 \pm 0.38	0.0001*
Hallux length without claw (mm)	5.86 \pm 0.33	6.17 \pm 0.28	0.0360*
Body weight (g)	6.6 \pm 0.35	6.3 \pm 0.52	0.0078*
Alula (mm)	11.2 \pm 0.42	11.65 \pm 0.83	0.2507
Live bird			
Wing aspect ratio	1.71 (1.51-1.87)	1.68 (1.51-1.82)	
Wing loading (g \cdot cm ⁻²)	0.13 (0.11-0.15)	0.13 (0.12-0.15)	

Ecology.—Two sets of ecological data (choice of substrate and locomotory feeding movements) were analyzed for differences between the kinglet species.

(1) *Choice of substrate.* Golden-crowned Kinglets showed a strong preference for feeding in conifers. Twenty of twenty-five (80%) feeding groups at Little Catawaqui Creek and twenty-two of twenty-five (88%) at Prince Edward Point were in conifers. The remainder were in low deciduous shrubs. For the Ruby-crowned Kinglet at Little Catawaqui (65 observations), 80% of the feeding groups were in deciduous and 20% in coniferous trees. At Prince Edward Point (48 observations), 55% were in deciduous trees and 45% in conifers. This suggests that the Golden-crowned Kinglet is a conifer specialist and the Ruby-crowned more of a generalist in substrate choice (see Bent 1949).

(2) *Locomotory feeding movements.* The species differed significantly in proportions of different foraging tactics used ($\chi^2 = 4.9$, $df = 4$, $P < 0.0001$; Fig. 3). Though foliage gleaning predominated in both species (39% of the Ruby-crowned and 42% of the Golden-crowned prey attacks), the Golden-crowned Kinglet fed much more by clinging to or hanging from the foliage. The Ruby-crowned Kinglet had a more pronounced aerial feeding component and fed more commonly by fluttering at or plucking prey from deciduous trees. Flight angles during feeding also differed significantly ($\chi^2 = 13.56$, $df = 4$, $P = 0.01$; Fig. 4). The horizontal component predominated in both species, being the main an-

gle of movement between foraging sites as well as during prey attacks. The two kinglets differed little in the upwards angle of feeding. However, the Golden-crowned used a higher percentage of angled flights in foraging overall, with a pronounced downward-angle component. The Ruby-crowned Kinglet exhibited a higher percentage of non-angled upward and horizontal flights. Flight distances during feeding of the two species did not differ significantly ($\chi^2 = 11.21$, $df = 8$, $P > 0.05$), although the Golden-crowned Kinglet tended to make more very short flights.

Search and prey-attack rates (hops per minute, flights per minute, and prey-attacks per minute) appear highly variable for each species (Table 3). However, the Golden-crowned Kinglet hopped significantly more frequently than the Ruby-crowned (*t*-test, $P < 0.05$).

DISCUSSION

The Golden-crowned and Ruby-crowned kinglets differ in a series of morphological features and most of these can be linked to differences in feeding behavior and substrate use. The Ruby-crowned Kinglet has a longer leg, and relatively longer tarsometatarsus. The tarsus tends to be longer in birds that utilize rigid perches (Grant 1971), and a longer tarsus probably favors exploitation of a wider range of resources (Grant 1971). On their wintering grounds, Ruby-crowned Kinglets show great variability in use of foraging substrates (leaf,

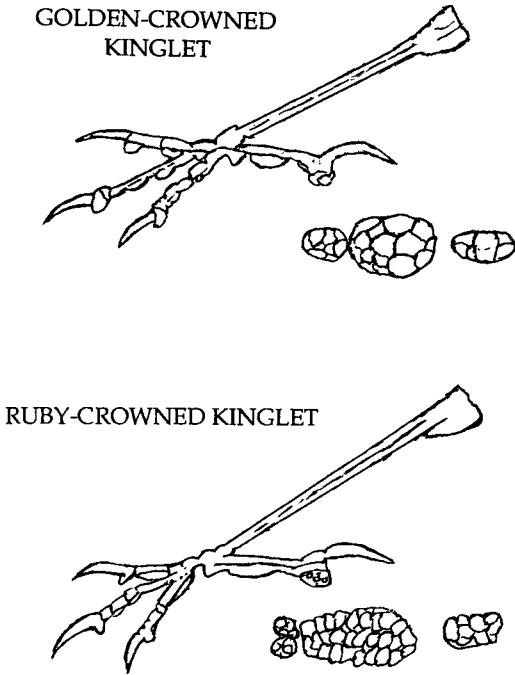


Fig. 2. Structure of the feet and toe pads of Ruby-crowned and Golden-crowned kinglets viewed from the side and underside; drawn and enlarged from live birds by Keast.

bark, flowers, ground) but are fairly restricted in size of perches used (Laurenzi et al. 1982). The tarsus tends to be shorter in birds that hang from slender branches (Palmgren 1932). These conclusions are consistent with the observation that Ruby-crowned Kinglets are less specialized in choices of perching substrates and with the prominence of clinging in the Golden-crowned Kinglet. However, the tarsus, more than any univariate measurement, is often an indicator of body size (Rising and Somers 1989, Freeman and Jackson 1990). The tarsus of the Ruby-crowned may also reflect its larger overall size. The relatively longer hind toe and hind claws of the Golden-crowned Kinglet are presumably an adaptation for clinging, as suggested for the European Goldcrest (Leisler and Thaler 1982) and for the Coal Tit (*Parus ater*) relative to the Blue Tit (*P. caeruleus*) (Partridge 1976). Differences in the soles of the feet appear to be exact counterparts of those found in the Goldcrest and Firecrest. Leisler and Thaler (1982) point out that the specialized structure of the Goldcrest's feet permits it to grasp and cling from pine needles. Presumably this also explains the

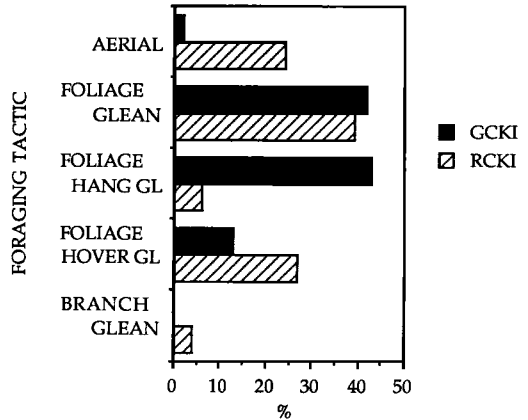


Fig. 3. Foraging tactics, Ruby-crowned (RCKI) and Golden-crowned (GCKI) kinglets, Little Cataraqui Creek and Prince Edward Point, Ontario, April to May, 1989. For explanation of categories see text.

specialized foot structure in the Golden-crowned Kinglet, which foraged predominantly in conifers.

The Ruby-crowned Kinglet has a relatively longer humerus than the Golden-crowned. Leisler and Thaler (1982) relate the relatively longer humerus of the Firecrest to longer and more sustained flights than the Goldcrest. The Ruby-crowned Kinglet has a longer wing than the Golden-crowned though neither measurements of wing chord nor lengths of the major primaries indicate this. Lengthening of the humerus and ulna concurrent with lengthening of the secondaries imply an increase in overall wing size and area. The longer secondaries of the Ruby-crowned Kinglet (the prime airfoils providing lift in birds) may function along with the longer humerus and ulna to allow longer aerial bouts. We found that aerial foraging is more important in this species. On the wintering grounds, Ruby-crowned Kinglets fed by hovering 25-35% of the time, and by hawking 5-10% of the time; the proportions varied only slightly over the season (Laurenzi et al. 1982). Wing loadings and aspect ratio are no different between the species. The need for maneuverability within vegetation during foraging may constrain both species to similar low aspect ratios and wing loadings (see Norberg 1986, Norberg and Norberg 1986, Rayner 1988). The alula, which produces high lift at very high angles of attack (Nachtigall and Kempf 1971) is not longer in the Ruby-crowned Kinglet than in the Golden-crowned Kinglet (Table 2). The Euro-

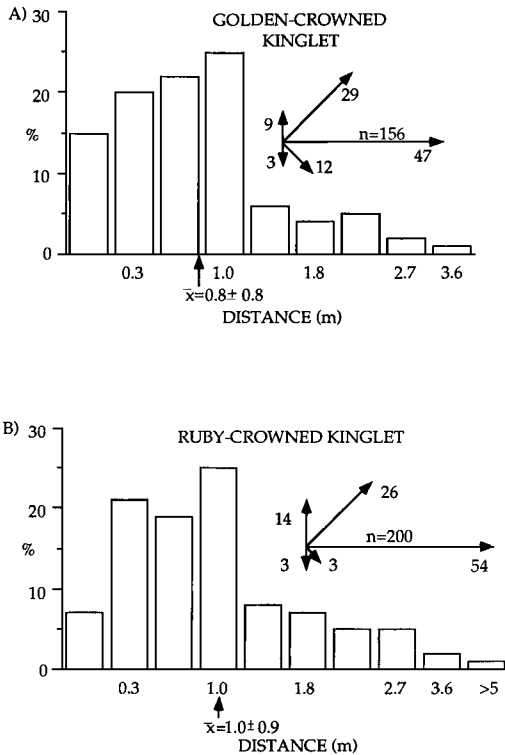


Fig. 4. Flight distances and angles when feeding in Ruby-crowned and Golden-crowned kinglets, April to May, 1989.

pean *Regulus* differ in this feature (Leisler and Thaler 1982).

The tails of small passerine birds are used mainly for steering, and longer outer tail feathers are particularly important. *Phylloscopus* species, especially those that take prey on the wing, tend to have short central feathers and longer outer ones (Gaston 1964). Tail length is not significantly different between the kinglet species (Table 2), but the tail of the Golden-crowned Kinglet is more forked. This seems anomalous relative to our findings that the Ruby-crowned Kinglet is the predominant aerial feeder. However, forking of the Golden-crowned Kinglet's tail may impart greater maneuverability, reflected in the higher percentage of angled foraging flights in this species. In Europe, the Goldcrest has the more forked tail, which may be related to different modes of hovering (Leisler and Thaler 1982). Goldcrests make short flights to hover in front of twig tips, whereas Firecrests switch from one twig to another, covering greater distances.

Generally, there is a positive correlation between size of bill and size of prey consumed (Hespenheide 1973, Lederer 1975, Smith and Zach 1979), and a larger bill favors taking prey of a wider range of sizes (Grant 1968, Herrera 1978). However, Hespenheide (1971) found that, in the Tyrannidae, body size predicts prey size better than bill size does, and Wiens and Rotenberry (1980) failed to find a correlation between bill and prey size in grassland birds. There is a direct relationship between bill length and speed at which the mandibles can be closed (Beecher 1962); longer-billed birds should capture fast-moving prey more readily. The greater force exerted by the longer bill may also improve handling of larger prey (Bock 1964, Lederer 1975). Most of these correlations remain untested functionally. Thaler (1988, pers. comm.) found no difference in sizes of prey consumed by the Ruby-crowned and Golden-crowned kinglets, but the Ruby-crowned prefers flying insects and the Golden-crowned prefers soft-bodied prey from the substrate.

Aerial-feeding birds characteristically have broadened bills and long rictal bristles. Leisler and Winkler (1985) showed positive correlations of bill width and bill length with rictal bristle length. Rictal bristles have been thought to function as a funnel that gives birds larger and more effective gapes (Lederer 1972, Stettenheim 1974), as protection for the eyes from food items the bird is trying to capture (Conover and Miller 1980) or as a sensory function (Stettenheim 1974). Lederer (1972) was unable to establish that they aid in prey capture in tyrannid flycatchers that capture the prey with the tip of the bill, and Conover and Miller (1980) found that taping the bristles down did not impede prey capture. Nevertheless, we suggest that the longer and broader bill and longer rictal bristles of the Ruby-crowned Kinglet are linked functionally with the demonstrated greater emphasis on aerial feeding in this species.

In many features the Ruby-crowned Kinglet and Firecrest, and Golden-crowned Kinglet and Goldcrest, are counterparts. Presumably the utilization of comparable ecological opportunities involved the humerus, rictal bristles, bill width, structure of the feet, claws, and soles of the feet in similar ways. In contrast, other features have evolved differently and the Ruby-crowned Kinglet has a significantly longer bill and longer tarsus than its North American congener.

TABLE 3. Search and prey-attack rates ($\bar{x} \pm SD$) of Ruby- and Golden-crowned kinglets. The number of feeding sequences (n) and the total number of minutes during which feeding was observed are given; * = significant t -test ($\alpha \leq 0.05$).

Species	n	Total min	Hops/min	Flights/min	Prey attacks/min
Ruby-crowned Kinglet	49	16.3	25.1 \pm 14.5*	9.3 \pm 6.6	9.3 \pm 8.2
Golden-crowned Kinglet	30	10.0	32.5 \pm 11.8	10.3 \pm 4.7	9.4 \pm 3.8

We cannot determine if the two North American *Regulus* are representative of the two Eurasian stocks, or if they were derived by double invasion of a single one. When compared with the data of Leisler and Thaler (1982), each North American species appears to be a partial ecomorphological equivalent of one of the Eurasian ones. Mayr (1956) pointed out the distinctiveness of the Ruby-crowned Kinglet and its strong differences from both Eurasian species in many features, as well as from the Golden-crowned Kinglet. We presume this indicates a long history in North America. Thaler (1990a, b; pers. comm.) has found that in the sum of behavioral patterns, postembryonic development, and postembryonic vocalizations, both American kinglets are more closely related to the European Firecrest than the Goldcrest. This could indicate that originally both were derived from the ancestors of modern Firecrest stocks.

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