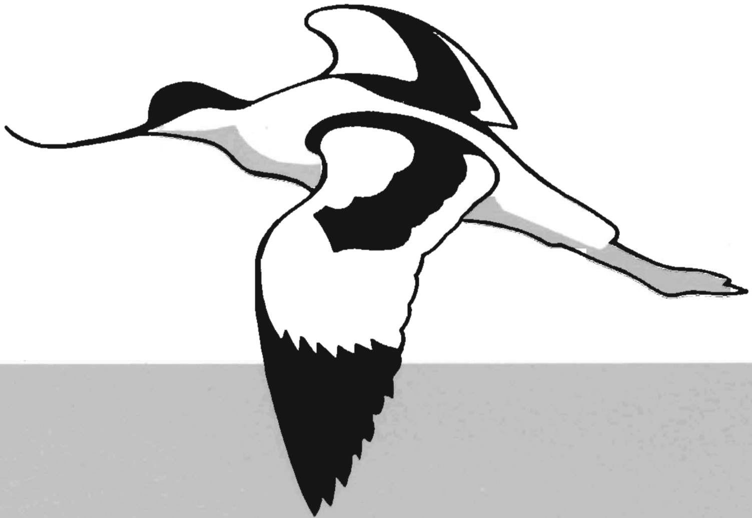
ISSN
0404-4266



AVOCETTA

Journal of Ornithology

CISO
Centro Italiano Studi Ornitologici

Volume 17 Dicembre 1993 N. 2

AVOCETTA

Journal of Ornithology

Published by the CISO

CISO

Centro Italiano Studi Ornotologici

Director	**Secretary**
P. BRICHETTI	N.E. BALDACCINI

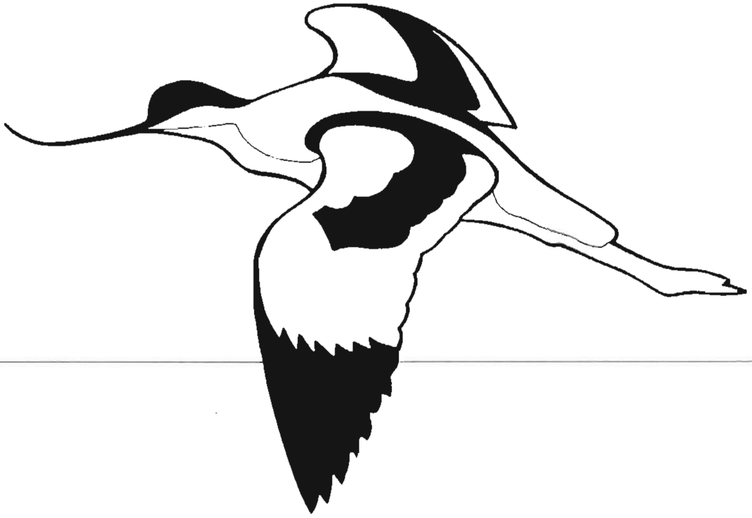
The CISO has the aim to stimulate and organize the ornithological research in Italy. All paid-up members of the CISO are entitled to receive Avocetta free. Applications for membership are welcome.
The journal appears in 1 volume per year, normally 2 issues per volume.
Subscription price for 1993 is Lit. 30000 and for 1994 Lit. 40000, post free.
Please write to the Secretary, Prof. N.E. BALDACCINI, Dipartimento di Scienze del Comportamento Animale, via A. Volta, 6 56126 Pisa, Italy.

Il CISO ha lo scopo di promuovere e organizzare la ricerca ornitologica in Italia. Tutti i membri del CISO in regola con il pagamento della quota associativa ricevono la rivista Avocetta. Per nuove richieste di associazione scrivere alla Segreteria, Prof. N.E. BALDACCINI, Dipartimento di Scienze del Comportamento Animale, via A. Volta 6, 56126 Pisa, Italy.
La rivista viene pubblicata in 1 volume ogni anno, normalmente con 2 numeri per volume.
La quota di iscrizione per il 1993 è di Lire 30000 e di Lire 40000 per il 1994, comprese le spese postali. Il pagamento deve essere inviato alla segreteria: Baldaccini prof. Natale Emilio, c/o DISCAU, via A. Volta 6, 56126 PISA - c.c.p. 14953566.

Avocetta viene pubblicato con il contributo finanziario di:
Parco Naturale Mont Avic, Champdepraz, Aosta
Dipartimento di Biologia Animale, Torino
Consiglio Nazionale delle Ricerche, Roma
Dir. Resp. S. Frugis, Autorizzazione Tribunale Parma n. 698, 11.4.1984.

Stampato da: Silvestrelli & Cappelletto s.r.l., via Romani 17F - 10131 Torino

ISSN
0404-4266



AVOCETTA

Journal of Ornithology

CISO
Centro Italiano Studi Ornitologici

Volume 17 Dicembre 1993 N. 2

Special issue

Recent advances in the study of the Apodidae

Editors:

Giorgio Malacarne
Dipartimento di Biologia Animale
Università di Torino, Italia

Charles T. Collins
Department of Biological Sciences
California State University,
Long Beach, USA

Marco Cucco
Dipartimento di Biologia Animale
Università di Torino, Italia

Dedication

to those who have gone before us:

D. Lack
H. Arn-Willi
E. Weitnauer
H. Sick
R. Dexter

Avocetta N° 17: 93 (1993)

Preface

Swifts are a well defined group of birds that are truly masters of the aerial environment. Many spend most of the daylight hours aloft in search of their arthropod prey, returning to terra firma only for nesting and roosting. Although they are found in both tropical and temperate areas around the world they are most abundan in tropical areas where up to six or more species may co-occur. Many temperate zone species are migratory, in some cases making impressively long transequatorial fligths to southern hemisphere wintering grounds. Despite the amount of published literature on swifts (>2500 titles) there is still much to be learned about these fascinating birds. Many nest in inaccessible rock crevices or in hard to locate hollows in forest trees thus greatly hindering detailed life history studies. For several species little is known other than distribution determined from a bare handful of museum specimens; a new specie was described as recently as 1992! Much of the difference in the estimates of the number of species in the family, ranging from 75 to 100, comes from the great difficulty in determining species limits in the echolocating cave swiftlets of southeast Asia and the pacific islands.

Swifts are fascinating but also, at times, extremely frustrating due to the difficulties in studying them compared to some more common and easily observed passerine species. Nonetheless, the rewards are great for the relatively small and widely scattered group of scientists who are preoccupied by these birds.

Current research on swifts takes many forms. For the five Palearctic species which have a long history of nesting in close association with humans the availability of study colonies with accessible nests has allowed data to be gathered answering increasingly sophisticated questions about breeding biology, feeding strategies, demography and survival. Elsewhere research continues on patterns of distribution, species and subspecies limits as well as patterns of genetic and karyotypic variation. The series of papers assembled here represent a cross section of the types of studies currently being conducted as well as a wealth of new information on many aspects of the biology of swifts. As ever, they will in turn be stepping stones for further advances in our knowledge of the Apodidae.

Giorgio Malacarne
Charles T. Collins
Marco Cucco
Editors.

Avocetta N°17: 95-100 (1994)

Taxonomic notes on the White-collared Swift (*Streptoprocne zonaris*)

KENNETH C. PARKES

Carnegie Museum of Natural History, 4400 Forbes Avenue - Pittsburgh, Pennsylvania 15213 USA

Abstract The White-collared Swift (*Streptoprocne zonaris*) is a large, gregarious, strongly-flying species found from Mexico and the Greater Antilles to Argentina, and from the Tropical to the Temperate Zone. Five subspecies were recognized in the standard check-list of Peters (1940), and an additional subspecies was described by Niethammer in 1953. This study of a series of 225 specimens shows that recognition of two previously synonymized subspecies was warranted. A large area of the Subtropical Zone of South America is occupied by a subspecies universally known in the literature as *albicincta*, but which does not match the holotype of that subspecies and is hence nameless; it is described herein as new.

The White-collared Swift *(Streptoprocne zonaris)* is a large, gregarious Neotropical species with a wide range, both geographic and altitudinal, from Mexico and the West Indies to northern Argentina, and from the Tropical to the Temperate Zone. It can be roughly described as a large, blackish swift with a prominent white collar, encircling the bird at the nape and upper breast. It is geographically variable; Peters (1940) admitted five subspecies. The only subsequent detailed discussion of variation in this species I have seen is that of Zimmer (1953). My study of 225 specimens, representing the combined series of 48 in the Carnegie Museum of Natural History (CM) and 177 (including 4 holotypes) in the American Museum of Natal History (AMNH), has led me to conclusions quite different from those of Peters or Zimmer, the most surprising discoveries being that the subspecies with the most extensive range lacks a valid name, and that the subspecies *albicincta* (Cabanis), assigned a range by Peters (1940) that extended from Honduras to Brazil, actually has one of the smallest ranges in the species.

The principal geographically variable characters of *Streptoprocne zonaris* are wing length (measurements, of adults only, in this paper are of the flattened wing; the sexes are alike in size and their measurements are pooled in the accounts below), relative blackness of plumage, presence or absence (and extent when present) of white edgings ("scalloping") on feathers of various tracts, and amount of development of the white collar that gives the species its name. Immature individuals within a given population tend to have the white collar less well developed, and pale or white feather edgings more widely distributed and conspicuous than on adults.

Although most of the subspecies can be reasonably well characterized and have distinct ranges, there are several specimens that appear decidedly "wrong" for their collection site. These will be mentioned beyond. Zimmer (1953) mentions possible migration in this species only in connection with a specimen from Mato Grosso, Brazil, citing early authors who believed that the species was only a transient in Trinidad and in Guyana. This is confirmed for Trinidad by ffrench (1991). Meyer de Schauensee (1966) mentions migration only in connection with the population of the mountains of northwestern Argentina, migrating to the provinces of Entre Ríos and Córdoba, information undoubtedly extracted from Olrog (1963).

The subspecies that appear to be separable are as follows:

Streptoprocne zonaris pallidifrons (Hartert)

Chaetura zonaris pallidifrons Hartert, Ibis, 1896: 368 (Jamaica; lectotype from Ferry River, St. Catherine designated by Hartert 1922:399). Syn: *Streptoprocne zonaris melanotis* Peters, Proc. New England Zool. Club 6,1916:37 (Sosúa, Dominican Republic); see Wetmore and Swales 1931:263.

Characters: Wing (n= 17) 193-206.5 mm. The most distinctively colored subspecies. The feathers at the base of the bill, at a minimum, are brownish gray; this color often extends somewhat onto the forehead or

Accepted 30 December, 1993

even the throat. The gray forehead area becomes whiter posteriorly, as a narrow white line encircling the black area that is just in front of the eye, and extending posteriorly above the eye to its midpoint at most. The throat in general is less intensely black than in mainland races. Adults have relatively inconspicuous pale buff (not white) scalloping on the marginal coverts. This is more conspicuous in immature birds, but these have no additional scalloping elsewhere.
Range: Cuba, Jamaica, Hispaniola (including Tortue Island); casual or accidental in the Isle of Pines (sight records), Vieques, and Lesser Antilles (fide Bond 1985).

Streptoprocne zonaris mexicana Ridgway

Streptoprocne zonaris mexicana Ridgway, Proc. Biol. Soc. Washington 23,1910: 53 (Rio Seco, near "Cordova, Vera Cruz" = Córdoba, Veracruz).
Characters: Very large (wing [n = 20] 204 [1 specimen], 206.5-217.5 mm). Throat and posterior underparts grayest of all races. White breastband broad. All of underparts of immatures lightly scalloped in fresh plumage.
Range: Mexico, north to Guerrero, San Luis Potosì, and Tamaulipas; Guatemala (Griscom 1932). The single specimen from Belize examined, and the variation in Belize specimens reported by Russell (1964) suggests intergradation with the following race; a series from Honduras is clearly intermediate (see beyond). Accidental at Perdido Key, southwesternmost Florida (Hardy and Clench 1982), where a White-collared Swift was found dead; observer reports suggest that it may have been part of a flock of 6 or 7. Also accidental on Padre Island, Kleberg Co., Texas, 8 March 1983 (Lasley 1984). The author identified the specimen only tentatively as *mexicana*, stating that it needed comparison with *pallidifrons* and *albicincta*. Its wing length of 211 mm. however, precludes its having been anything except another example of *mexicana*. A White-collared Swift photographed on the Texas Gulf Coast near Surfside, Brazoria Co., Texas, 19 December 1987. was probably *mexicana* (Eubanks and Morgan 1989). The latter paper mentions several sight records of "large black swifts" along the Texas coast in December 1987, suggesting the possibility that there was a northward movement of White-collared Swifts from Mexico during that month. Much farther from the breeding range of *mexicana* (or any other race) was a swift sketched and well described at Point St. George, Del Norte Co., California, 21 May 1982 (Erickson et al. 1989). Although the locality was such an unlikely one, there is little doubt that the bird was a White-collared Swift, and the record has been accepted as such by the California Bird Records Committee.

Streptoprocne zonaris bouchellii Huber

Streptoprocne zonaris bouchellii Huber, Auk 40,1923:302 (Eden, Lat. 14°00'N, Long. 84°26'W, Nicaragua).
Characters: Wing [n = 14] 195 [1 specimen], 200-210, thus almost as large as *mexicana* (measurements given by Huber [1923] of 191-205 were undoubtedly of the chord rather than the flattened wing). Distinctly blacker below than *mexicana*; breastband narrower in adults and much narrower, even rudimentary, in immatures. Immatures with scalloping on the throat; barely visible if at all present on rest of venter.
Range: Nicaragua through Panama. Intergrades with *mexicana* in Belize and possibly part of Guatemala; Russell (1964) examined 4 Belize specimens and called 2 of them *mexicana* and 2 "*albicincta*". A series of 17 from Honduras in CM shows complete mixing of *mexicana* and *bouchellii* characters. Monroe (1968) recognized this intermediacy, but (as did Russell) wrongly attributed the southern element in the intergrades as "*albicincta*," a race alleged by Peters (1940) to range from Honduras to Brazil. Wetmore (1968) called Panama birds "*albicincta*," but his account does not suggest that he made any critical study of geographic variation in the species.
Remarks: This subspecies has been synonymized with *albicincta* (Cabanis) ever since it was discussed by Peters (1929). In Huber's words, *bouchellii* was "similar to *S. z. albicincta*, but white collar in front decidedly narrower and much less white, only the tips of the lower throat feathers for about 3 millimetres being white, rest of the feathers sooty blackish, presenting an indistinct and mottled collar, in some specimens the collar is barely traceable." Peters (1929) dismissed this character as being based on "age or individual variation." He did not specify how many Nicaragua specimens he examined to come to this conclusion; his remarks were made in connection with identifying what was then the first specimen from Honduras. For Peters to have been correct would necessitate all 8 of Huber's series, shot (presumably at random) between 25 March and 1 April 1922, to have been immature birds, which would seem unlikely. Peters and those authors who have followed him in synonymizing *bouchellii* (e.g., the dogmatic statement of Griscom [1932]) have overlooked the fact that whereas the development of the white breastband is indeed less in immatures than in adults, the amount of white is also geographically variable. This is well illustrated by Huber's noting that "in some specimens

the collar is barely traceable," these being with little doubt the actual immatures in his series. In the CM Honduras series of *mexicana-bouchellii* intergrades, this extreme condition appears in two immature specimens. CM 133697, San Esteban, Olancho, is nearest *bouchellii* in general body color, and CM 135381,10 km N Sabana Grande, Morazan, is nearest *mexicana*, but both have the breastband much reduced; in the case of 133697, it is only one feather deep at the center. In no other subspecies except the much smaller *minor* of Venezuela (not recognized by Peters) is the breastband as reduced in both age classes as it is in *bouchellii.*

Streptoprocne zonaris minor (Lawrence)

Hemiprocne minor Lawrence, Ann. New York Acad. Sci. 2, 1882:355 ("Bogotá = error for Trinidad; see beyond).

Characters: Wing (n= 15) 180 [1 specimen], 183-197 mm., thus one of the smallest races. White breastband reduced, in this character exceeded only by the larger race *bouchellii*; in almost all adult specimens, the white is confined to the tips of the feathers such that the breastband appears mottled; breastband of immatures correspondingly even more reduced. Throat rather grayish. White or whitish edgings in adults usually confined to marginal wing coverts, where they are fairly conspicuous; very narrow white edgings are present on tips and inner margins of inner remiges, disappearing or almost so with wear. Immatures have the most extensive scalloping (although it is narrow) of any race except the large *kuenzeli* of the Bolivian highlands; on extreme individuals it is present on throat, abdomen, flanks, and upper and under tail coverts as well as on the marginal coverts of the wing.

Range: Coastal mountains of Venezuela, frequently found in Trinidad where not yet known to nest (ffrench 1991); Collins (pers. comm.) considers this movement as straying rather than a regular migration.

Remarks: Naumburg (1930) pointed out that Lawrence's holotype of *minor* from "Bogotá" (which I have examined at the American Museum of Natural History) was not of the well-known "Bogotá" trade skin make, but instead matches "the well-known Orinoco or Trinidad make". This was reiterated by Zimmer (1953), who pointed out its resemblance to other Trinidad specimens. These clearly belong to the subspecies of the coastal mountains of Venezuela; the holotype differs only in having a flat wing measurement of 180 mm, 3 mm shorter than any mainland specimen (its wing length is cited by Zimmer and others as 178 mm, but he undoubtedly did not flatten the wing fully on the ruler). I have no hesitation in accepting Zimmer's tentative suggestion, and restrict the type locality of *Hemiprocne minor* Lawrence to Trinidad. ffrench (1991) believed that the swifts of this species seen in Trinidad represented "a post-breeding dispersal, probably from the Venezuelan Andes." Birds from those mountains, however, belong to a different subspecies than do the available Trinidad specimens; as the latter are matched by those of the coastal mountains, the name *minor* will apply to the coastal and not the Andean birds.

Streptoprocne zonaris albicincta (Cabanis)

Hemiprocne albicincta Cabanis, Journ. f. Orn. 10, 1862:165 (Mexico to Guiana; restricted to the junction of Haiama Creek and the Demerara River, British Guiana [= Guyana] by Zimmer [1953]).

Characters: Wing [n= 15] 182-197 mm, thus similar in size to *minor*, but much blacker in color. Almost no feather edgings visible, even in immatures. Immatures have some scalloping on the throat, but on the rest of the underparts scalloping is barely visible, if present at all, and brownish rather than white when present. Breastband of adults broad.

Range: Guyana; most of Venezuela except the coastal mountains and the Andes; Tropical Zone, extending into Subtropical in the Tepuì region.

Remarks: This name has been used by most authors, following Peters (1940), for the White-collared Swifts of a huge area from Honduras to Peru and Mato Grosso. Most specimens from this range, however, do *not* match those from Guyana, the type locality, and the range of true *albicincta* is thus much smaller. Like other populations of this highly mobile species, members of *albicincta* apparently migrate or wander into areas within the breeding range of other races. A group of 5 specimens (AMNH) from "Rancho Grande" (Henri Pittier National Park), Venezuela, cannot be separated from *albicincta* specimens from Guyana and the Tepuì region, although this locality is in the coastal range, only about 80 km west of Petare, the source of a series of *minor* in CM. On the other hand, AMNH 188183, a specimen from Mt. Turumiquire, NW Monagas, at the base of the Paría Peninsula, is neither *minor* nor *albicincta*, being much too large for either (wing 210 mm). It is quite dark, but somewhat brownish on the forehead. It has a very well developed, adult-type breastband, well developed scalloping on the marginal wing coverts, and faint traces of pale scalloping and tipping on the posterior underparts and greater wing coverts. It resembles nominate *zonaris* in size, but differs in color, and matches no other known subspecies.

Streptoprocne zonaris zonaris (Shaw)

Hirundo zonaris Shaw, in J. F. Miller's Cimelia Physica, 1796:100, pl. 55 [not seen]. (No locality, but assumed to be Brazil; see beyond).

Characters: A large (wing [n= 18] 204-221 mm.), very dark race, adult with no scalloping on the marginal wing coverts; breastband not especially wide, and tending to be interrupted or narrowed where it joins the nape portion of the "collar"; white tips of breastband feathers narrow, so that worn birds show the black bases of these feathers. Immatures with the least pale scalloping of any race; marginal wing covert edging brownish, and with virtually no other traces of edgings, barely visible with a hand lens on the throat of one and the abdomen of another, brownish, narrow, with almost no contrast to the rest of the feather.

Range: Tropical lowlands from Bolivia through Brazil. Meyer de Schauensee (1966) does not mention Paraguay in the range of this species, but the AMNH has 3 specimens from "east of Caaguazú Alt. 1000 ft." (Naumburg 1935), in easternmost Paraguay. Narosky and Yzurieta (1987) indicate that it is absent from Uruguay. Cuello and Gerzenstein (1962) mentioned a mounted specimen said to have been obtained in the vicinity of Montevideo in 1934.

Remarks: Past authors have generally agreed that the type specimen of Shaw's *Hirundo zonaris*, described without a definite locality, probably came from Brazil. Chapman (1914) reviewed earlier suggestions as to the provenience of Shaw's bird, and then restricted the type locality to "Chapada, Matto Grosso, Brazil." Having, in this same paper, described an Andean subspecies, Chapman wrote "It is most unlikely that Shaw, writing in 1796, had specimens of the Swift of the High Andes." However, Naumburg (1930) quotes Hellmayr (apparently in a pers. comm.) as indicating that Shaw's type did not come from Chapada, as in Shaw's time the province of Mato Grosso was practically unknown. He suggested Rio de Janeiro as a more likely source for Shaw's specimen, a designation accepted by Naumburg. Later, Peters (1940) called Chapada "a very improbable locality" and cited Naumburg (1930), but did not substitute Rio de Janeiro. I find the suggestion of Hellmayr and Naumburg eminently sensible, and accept the restricted type locality of *Hirundo zonaris* Shaw as Rio de Janeiro, Brazil.

Naumburg (1930) identified a single specimen from Utiarity, Mato Grosso, as an adult of "*albicincta*", with a wing length of 174 mm. I remeasured it, with the wing flattened to be comparable with my other measurements, and found that the two wings differed slightly, the flat measurements being 175 and 177 mm. If it is indeed an adult, it is the smallest *Streptoprocne zonaris* measured in this study (a specimen of *minor* from Trinidad with a wing of 178 was labeled "juv." by the collector). The smallest *albicincta* measured had a wing of 182 mm.; it is conceivable that the Utiarity bird could be an especially small (immature?) *albicincta*, but that race, as here restricted, has a broad breastband, whereas that of the Utiarity bird is exceedingly narrow, the collar on the nape is only about 2 feathers wide, and is all but invisible because of the compressed "make" of the skin. Rather than following Naumburg in assigning this specimen to *albicincta* I find myself agreeing with Zimmer (1953), who believed that the Utiarity bird might represent a migrant or stray of a breeding population from an as yet unknown breeding area, probably to the north. Zimmer (1953), in commenting on this small specimen, stated that there was only this "single bird from northern Mato Grosso." However, there are 4 specimens in the AMNH from Chapada, Mato Grosso (Naumburg 1930; Zimmer [1940] lists 3), undoubtedly why Chapman chose this for his type locality restriction. Utiarity is only a little more than 300 km north of Chapada (map in Naumburg 1930), and both are on tributaries of the Rio Madeira, so it would appear highly unlikely that there is any significant zoogeographic difference between the two localities such that breeding birds from Chapada and Utiarity might be expected to differ subspecifically.

Streptoprocne zonaris altissima Chapman

Streptoprocne zonaris altissima Chapman, Bull. Amer. Mus. Nat. Hist. 33,1914:604 (Laguneta, alt. 10,300 ft., near Quindio Pass, Central Andes, Colombia).

Characters: Wing 220+ (worn), 223, 224, 226, 227.5, 232 (all from Ecuador). An exceedingly distinctive subspecies. It not only includes the largest individuats of the species, but also has the broadest collar in the species, being continuous around the neck rather than narrowing at the nape or sides of neck. Adults have distinct white scalloping on the marginal wing coverts; scalloping of immatures narrow but white and well contrasting, both on the throat and the venter. General color blackish, throat little if any paler than breast. Chapman described *altissima* as "general color, particularly of the inner wing quills and wing-coverts greener" than. in *zonaris*. I could not see this at all; for example, a skin of *zonaris* from Rio Grande do Sul, Brazil, is greener than any *altissima* seen. Collins (pers. comm.) has pointed out to me that in swifts a greenish gloss regularly wears to purplish (and then to no gloss at all) during a yearly cycle.

Range: High elevations (Temperate Zone) in Ecuador and the Central Andes of Colombia.

Remarks: Chapman (1914) gave the wing length of the holotype (AMNH 111521) of *altissima* as 212 mm. (presumably the chord). The flattened wing of this specimen measures 216 mm., but the outermost primary is worn, and probably lacks 1-2 mm., giving an estimated wing length of perhaps 218 mm. This is still somewhat shorter than the wing of the shortest Ecuador specimen measured (220 +, worn), but the Colombian and Ecuadorean birds are alike in color. Although in his original description, Chapman (1915) stated that he had only a single specimen from the type locality in Colombia, there are 2 topotypes in the AMNH. Unfortunately both of these birds were in molt, and their wings are unmeasurable. Chapman correctly emphasized that this swift is among those species having altitudinal subspecies in South America, even though they have, as he put it, "exceptional powers of flight."

Streptoprocne zonaris kuenzeli Niethammer

Streptoprocne zonaris künzeli Niethammer, Bonn. Zool. Beitr. 4,1953:286 (Puri [1200 m], Yungas von La Paz, Bolivia).

Characters: Wing ad. male 206, 211, 211+ [worn]; ad. female 211, 213; imm. male 208; imm. female 195,199, thus similar in size to *S. z. zonaris* of the adjacent lowlands. For comparison, CM specimens from 350-500 m in eastern Bolivia, ad. male 216; ad. female 204, 209, 211, 212; ad. sex ? 214; imm. female 195). Distinctively colored, especially the immatures, which are very heavily scaled all over; all remiges white-edged, even the crown with white edgings; very faint edgings on mid-back soon wear away, but conspicuous in all other areas. A strong white superciliary and lores. Adults differ from *zonaris* in having well-marked scalloping on marginal wing coverts, and 4 of 6 adults seen retained a narrow white superciliary; the general throat and underparts color somewhat brownish, not blackish as in *zonaris*. Niethammer's wing measurements were male 209, female 198,199, 204. These probably represent the chord of adults, as his measurements of females match mine of the flat wing of immature females; had he seen immatures, he surely would have commented on their unique coloration.

Range: High elevations in the Andes of Bolivia and adjacent northwestern Argentina (specimens examined from Tucumán Province).

Remarks: Article 32d (i) (2) of the International Code of Zoological Nomenclature requires that the umlaut in the original spelling of *künzeli* be changed to ue.

Streptoprocne zonaris subtropicalis, new subspecies

Holotype: CM 44856, adult male, collected at Pueblo Viejo, north slope of the Sierra Nevada de Santa Marta, alt. 2000 feet, Subtropical Zone (Todd and Carriker 1922:122) by M. A. Carriker, Jr., 6 March 1914 (Collector's no. 14191).

Characters: This is the subspecies that occupies most of the South American part of the range attributed to "*albicincta*" by Peters (1940) and subsequent authors. It differs from true *albicincta* most noticeably in size; wing length 194-207 mm versus 182-196 in *albicincta*. Resembles *albicincta* in general intensely black color and broad breastband; differs in adults often having scalloping on marginal wing coverts, white when present (usually wholly absent in adults of *albicincta*), and light scalloping on throat and underparts of immatures, sometimes but not always confined to the rear half of the body; in *albicincta* immatures may have some scalloping on the throat, but it is barely visible if at all present on the rest of the underparts, and is brownish when present. Blacker than the dark but dull, larger race *zonaris* of the Tropical lowlands to the east.

Range: Middle elevations in the Sierra Nevada de Santa Marta, Colombia, and the Andes from the Cordillera de Mérida in Venezuela south to Peru, principally in the Subtropical Zone.

Remarks: Two specimens from Urubamba Cañon, Cuzco, Peru (AMNH 145001 female, 145002 male) are duller and have wings 212 and 211 respectively; these may be intergrades with *zonaris*. This locality was listed as "not located" by Stephens and Traylor (1983), but they also stated that it was "downstream some distance from Machu Picchu." They give the elevation along the river at the base of the ridge at Machu Picchu as 2130 m, "lower subtropical forest." Urubamba Cañon, being downstream from Machu Picchu, is at least approaching the Tropical Zone. Also a possible intergrade with *zonaris* is AMNH 185209, a male (wing 210) from "San José Abajo" (= San José Nuevo, fide Paynter and Traylor 1977), Napo, Ecuador. Chapman (1926) states that this locality was at the lower border of the Subtropical Zone.

Acknowledgments - As always I am grateful to the authorities of the Department of Ornithology, American Museum of Natural History for permission to use their facilities. Charles T. Collins and M. Ralph Browning critically read an earlier draft; their suggestions improved the manuscript greatly.

Riassunto - *Streptoprocne zonaris* è una specie gragaria, di grosse dimensioni, che si trova dal Messico e le Grandi Antille fino all'Argentina e dalla zona tropicale a quella temperata. Peters (1940) ha descritto cinque sottospecie e Niethammer (1953) una successiva. Questo studio, basato su 225 esemplari,

dimostra che una sottospecie attualmente sinonimica deve essere distinta in due. Infatti una grande area della Zona subtropicale del sud America è occupata da una sottospecie nota universalmente come *albicincta*. Tuttavia essa non corrisponde all'olotipo della sottospecie e dunque rimane senza nominativo. La nuova sottospecie viene denominata *Streptoprocne zonaris subtropicalis*.

References

Bond J. 1985. Birds of the West Indies, 5th ed. *Collins, London*, 256 pp.

Chapman F. M. 1914. Diagnoses of apparently new Colombian birds. III. *Bull Amer. Mus. Nat. Hist.* 33: 603-637.

Chapman F. M. 1926. The distribution of bird-life in Ecuador. *Bull. Amer. Mus. Nat. Hist.* 55: xiv + 784 pp.

Cuello J. and Gerzenstein E. 1962. Las aves del Uruguay. *Com. Zool. Mus. Montevideo* 6:191 pp.

Erickson R. A., Morlan J. and Roberson D. 1989. First record of the White-collared Swift in California. *Western Birds* 20:25-31.

Eubanks T. L. Jr., and Morgan J.G. 1989. First photographic documentation of a live White-collared Swift (*Streptoprocne zonaris)* from the United States. *Amer. Birds* 43: 258-259.

ffrench R. 1991. A guide to the birds of Trinidad and Tobago, 2nd edition. *Cornell University Press, Ithaca*, NY: xx + 426 pp.

Griscom L. 1932. The distribution of bird-life in Guatemala. *Bull. Amer. Mus. Nat. Hist.* 64: x + 439 pp.

Hardy J. W.and Clench M.H. 1982. First United States specimen of the White-collared Swift. *American Birds* 36:139-141.

Hartert E. 1922. Types of birds in the Tring Museum. B. Types in the general collection. *Novitates Zoologicae* 29: 365-412.

Huber W. 1923. Two new birds from Nicaragua. *Auk* 40: 300-302.

Lasley G. W. 1984. First Texas specimen of the White-collared Swift. *Amer. Birds* 38: 370-371.

Meyer de Schauensee R. 1966. The species of birds of South America and their distribution. *Acad. Nat. Sci. Philadelphia*: xviii + 578 pp.

Monroe B. L. Jr. 1968. A distributional survey of the birds of Honduras. *Ornith. Monogr.* 7: 458 pp.

Narosky T. and Yzurieta D. 1987. Guía para la identificación de las aves de Argentina y Uruguay.*Vazquez Mazzini, Buenos Aires*: 346 pp.

Naumburg E. M. B. 1930. The birds of Matto Grosso, Brazil. *Bull. Amer. Mus. Nat. Hist.* 60: iii + 432 pp.

Naumburg E. M. B. 1935. Gazetteer and maps showing collecting stations visited by Emil Kaempfer in Eastern Brazil and Paraguay. *Bull. Amer. Mus. Nat. Hist.* 68: 449-470.

Niethammer G. 1953. Zur Vogelwelt Boliviens. *Bonn. Zool. Beitr.* 4:195-303.

Olrog C. C. 1963. Lista y distribución de las aves Argentinas. *Opera Lilloana* 9: 379 pp.

Paynter R. A. Jr. and Traylor M. A. Jr. 1977. Ornithological gazetteer of Ecuador. *Mus. Comp Zool., Cambridge, Massachusetts*: vii + 152 pp.

Peters J. L 1929. An ornithological survey in the Caribbean lowlands of Honduras. *Bull. Mus. Comp. Zool.* 69: 397-478.

Peters J. L. 1940. Check-list of birds of the world, vol. 4. Harvard Univ. Press, Cambridge, Massachusetts: xii + 291 pp.

Russell S. M. 1964. A distributional study of the birds of British Honduras. *Ornith. Monogr.* 1:195 pp.

Stephens L. and Traylor M.A. Jr. 1983. Ornithological Gazetteer of Peru. *Mus. Comp. Zool., Cambridge, Massachuetts:* vi + 273 pp.

Todd W. E. C and Carriker M.A. Jr. 1922. The birds of the Santa Marta region of Colombia. *Ann. Carnegie Mus.* 14: viii + 611 pp.

Wetmore A. 1968. The birds of the Republic of Panama, part 2. *Smithsonian Misc. Coll.* 150, part 2: vi + 607 pp.

Wetmore A. and Swales B.H. 1931.The birds of Haiti and the Dominican Republic. *Bull. U. S. Nat. Mus.* 155: iv + 483 pp.

Zimmer J. T. 1953. Studies of Peruvian birds. No. 64. The swifts: family Apodidae. *Amer. Mus. Novit.* 1609: 20 pp.

Avocetta N° 17: 101-106 (1993)

Species limits of the cave swiftlets *(Collocalia)* in Micronesia

M. Ralph Browning

National Biological Survey, MRC-116, National Museum of Natural History
Washington D.C. 20560 U.S.A.

Abstract - Cave swiftlets *(Collocalia)* from the Mariana, Caroline, and Palau islands build different types of nests and differ morphologically from each other and from *C. vanikorensis*. Populations from the three respective island groups are here considered specifically distinct from *C. vanikorensis* and each represent the following separate species: *bartschi, inquieta,* and *pelewensis*.

Introduction

Cave swiftlets *(Collocalia)*, a group of small swifts (Apodidae), breed on islands from the western Indian Ocean to the central Pacific and mainlands of southeastern Asia and Australia. Peters (1940) recognized three species of *Collocalia* from Micronesia. Mewday (1975) considered the Micronesian taxa *bartschi* of the Mariana Islands, *inquieta, rukensis,* and *ponapensis* of the Caroline Islands, and *pelewensis* of Palau as subspecies of *Collocalia vanikorensis* on the basis of their similar nests and morphology. Most authors (e. g.: Pyle and Engbring 1985, Pratt *et al.* 1987) follow Medway (1975). However, the types of nests of the taxa from Micronesia are not uniformaly similar to *C. vanikorensis*. The taxa *bartschi, inquieta* (with *rukensis* and *ponapensis*), and *pelewensis* differ morphologically from one another and *C. vanikorensis*, and are here treated as separate species. Sibley and Monroe (1990), citing my personal communication, listed the same taxa as allospecies of *vanikorensis*. Use of the generic name *Collocalia* instead of *Areodramus*, a name widley in current use, follows Salomonsen (1983) and others (e. g., Marle and Voous 1988, Sibley and Monroe 1990). The ranges and type localities of the taxa discussed are summarized in Table 1.

Table 1. List of type localities (in parenthesis) and ranges of *Collocalia* in this paper.

- *C. vanikorensis*[a] - Celebes, Moluccas, New Guinea to New Hebrides
  - *C. v. vanikorensis* (Island of Vanikoro) - New Hebrides
  - *C. v. waigeuensis* (Island of Waigeu) - Morotai and Halmahera in norther Moluccas, Misoöl, Waigeo, Batanta islands
  - *C. v. moluccurum* (Banda Island) - Banda Ils. in Moluccas, Ambon, Serem Laut Tajandu, and Kai islands
  - *C. v. pallens* (Dyaul Island) - Bismarck Archipelago
  - *C. v. lihirensis* (Lihir Island) - Hirberman and Nuguria islands
- *C. salangana*[b] (Java) - Greater Sundas
- *C. pelewensis* (Palau Islands) - Palau Islands
- *C. inquieta inquieta* (Kusaie Island) - Caroline Ils., Kosrae I.
  - *C. i. rukens* (Ruk Island) - Truck I.
  - *C. i. ponapensis* (Ponapé) - (now) Pohnpei
- *C. bartschi* (Guam) - Mariana Ils.; introduced in Hawaii[c]
- *C. germani*[d] (Conchinchina) - coasts of Malay Peninsula, Borneo, Palawan

[a] Sensu Solomonsen (1983)

[b] *Collocalia (fuciphaga) fuciphaga* of Peters (1940; see Medway 1961). Considered specifically distinct from *C. vanikorensis* by Dickinson (1989).

[c] American Ornithologists' Union (1983)

[d] Subspecies of *C. fuciphaga* of Medway (1966); but see Solomonsen (1983) and Bruce, in White and Bruce (1986)

Accepted 30 December, 1993

Table 2. Summary of the taxonomic history of the Micronesian *Collocalia*.

Source	*bartschi*	*inquieta*	*pelewensis*
Mayr (1937)	in *C. germani*	species	in *C. germani*
Peters (1940)	in *C. inexpectata*[a]	species	in *C. inexpectata*
Medway (1966)	in *C. vanikorensis*	species	in *C. vanikorensis*
Medway (1975)	in *C. vanikorensis*	in *C. vanikorensis*	in *C. vanikorensis*
Solomonsen (1983)	species	species	in *C. barschi*
This study	species	species	species

[a] *C. fuciphaga* of Medway (1966)

Taxonomic History

Classifications of *Collocalia* are summarized in Table 2. Earlier authors relied entirely on morphological characters. Mayr (1937:17-18) stated "it seems that the ... "races" *(pelewensis and bartschi)* "belong to *(C.) germani*·... "and commented that *C. inquieta* and *C. vanikorensis* may be conspecific. Peters (1940:220) adapted "the best features of the various reviewers (cited therein) of the genus ..." Mayr (1945), Baker (1951), and Brandt (1966) followed Peters. Medway (1966, 1975) focused less on morphology and more on ecology and behavior, especially nest structure. Salomonsen (1983) relied on both morphology and nest types.

Methods

Standard measurements of wing chord, tail length, their ratios, and other information are from museum study skins unless otherwise stated. A dissecting scope was used for examining tarsi.

Results

Morphology

Medway (1966, 1975) characterized *C. vanikorensis* as 115-126 mm in wing chord, pale gray with dark shaft stripes ventrally and blackish brown dorsally with the concealed barbs (rami) on the back white in the *vanikorensis* group and black in the *salangana* group. The wing chord of *C. vanikorensis* (excluding the *salangana* group) actually ranges from 109 (*waigeuensis*) to 127 (*lihirensis*) (see Mayr 1937; Salomonsen 1983). Of 12 subspecies in *C. vanikorensis* only *waigeuensis* was characterized by Salomonsen (op cit.) as lacking dark shaft-streaks, and *pallens* as having a pale rump. However, specimens of *waiguensis* from Halmahera (USNM) have dark shaft streaks and *pallens* is also paler on the upper back than the other subspecies in *C. vanikorensis*. The tarsi of *C. vanikorensis* is usually bare but feathers are present in some populations and individuals.

Several morphological characters (Table 3) in *C. vanikorensis* and the taxa from Micronesia differ.

Collocalia bartschi (wing 100-108) is smaller and, based on its ratio of wing chord and length of tail, has a proportionally longer tail than subspecies in *C. vanikorensis*. The plumage of *C. bartschi* differs from *C. vanikorensis* in lacking dark ventral streaks and the supraloral spot is very small or lacking. The density of the feathers on the tibia adjacent to the tarsus is noticeably greater in *C. bartschi* than in the other Micronesian taxa and *C. vanikorensis*. Seven of 10 specimens of *C. bartschi* have bare tarsi; three have single feathers on the middle of one tarsus. The tarsi of *C. pelewensis*, *C. i. ponapensis*, and *C. i. rukensis* are bare (Mayr 1935; pers. obsv.). I found one specimen of nominate *inquieta* with a single feather on the inside of its tarsus. The wing chord in the Caroline Islands population (*C. inquieta*) varies (*rukensis*, 103-109; *ponapensis*, 96-119; *inquieta*, 110-120), but the tail is proportionally longer than in *C. pelewensis* and *C. vanikorensis*. Specimens of *C. inquieta* are darker throughout, with the supraloral spot smaller, the auricular region darker, and the throat less silvery than that of typical *C. vanikorensis*. *Collocalia pelewensis* differs from the other Micronesian taxa and *C. vanikorensis* by its pale rump (with darker back) and proportionally short tail. It also differs from *C. bartschi* in wing chord (107-113) and paler auricular region. The tail/wing ratio of *C. pelewensis* (mean, 0.44) does not overlap that of *C. bartschi* (0.48) or *C. inquieta* (0.49) and overlaps only slightly with that of nominate *vanikorensis* (0.46) (Table 3).

Table 3. Morphological characters of some Pacific Island species of *Collocalia*.

	Species			
Character[a]	*vanikorensis*[b]	*bartschi*	*inquieta*	*pelewensis*
feathers on tarsi	none	30%	2%	none
supraloral spot	1	3	2	3
pale auricular	2	2	3	3
pale throat	1	2	3[c]	2
ventral streaks	1	3	2	2
dorsal sheen	1	3	2	2
tail/wing ratio	.45-.48	.47-.51	.47-.53	.41-.46
means±S.D.	.467±.009	.489±.018	.494±.012	.440±.018
number	19	12	46	6

[a] 1 = obvious, 2 = less obvious, 3 = nearly or completely absent

[b] Nominate subspecies

[c] Some individuals of *ponapensis* have pale throats (Mayr 1935)

Statistical (Student t-test) differences between the means of the ratios are significant ($P<0.05$) between *vanikorensis, pelewensis,* and between the similar means ($P>0.05$) of *bartschi* and *inquieta*. Two subspecies in *C. vanikorensis* (*moluccurum* and *waiguensis*) are similar to *C. pelewensis* in wing chord and relative tail length, but differ in plumage pattern and some individuals have feathers on the tarsi.

Type of nest

Medway's (1966) characterizations of the nests of the cave swiftlets were based mainly on the literature and nests in museum collections. He described the nest of *C. vanikorensis* as somewhat rounded, tending to be bracket-shaped, and composed of vegetable material held together with sparse to moderate amounts of "firm" (becomes hardened) mucilaginous nest-cement. He (Medway 1975) later described the nest of nominate *vanikorensis* as bound together with moist nest- cement, and stated that the same type of nest is built by *bartschi*, *inquieta*, *ponapensis*, and *rukensis*; Medway (1966) had earlier considered *C. pelewensis* as a subspecies of *C. vanikorensis* even though the nest was unkown. Based on the most recent classification of the types of nests (Medway and Pye 1977), the nest of *C. vanikorensis* is externally supported (attached to or supported by rock outcrops or cracks vs. self-supported) and consists of sparse amount (vs. moderate or copious) of moist (vs. hardened) nest-cement.

The nest of *C. bartschi*, characterized by Jenkins (1983), is "composed of moss tightly held together and firmly secured to cave walls with copious amounts of hardened mucus-like saliva." He also stated that the nests were often cone-shaped, and high above the cave floor, adding that "cave ceilings appear to be the preferred sites." According to J. Reichel (pers. comm.), the nests in the Marianas are usually externally-supported, but occasionally are self-supported and contain sparse to copious amounts of nest-cement. A nest of *C. bartschi* in Hawaii, where the species was introduced from Guam in 1962 (see beyond), was composed of vegetable material consisting mostly of a liverwort (*Herbertia* sp.) and sparse nest-cement, and all of the nests observed were supported by niches in the cave walls (J. Engbring, pers. comm.).

The nests of members of the *inquieta* group may be externally or self-supported, and consist of sparse or copious nest-cement. For example, Medway (1966) cited Brandt's (1962) description of nests of *rukensis* as held together by copious amounts of cement and that the nests are both externally and self-supported. Brandt (1966) also characterized the nest of *rukensis* as "deeply cupped" and rarely consisting of moss, the nests of other members of *C. inquieta* as consisting mostly of moss held together with a minimal amount of nest-cement and with shallow cups. Brandt (1966:63) considered the nest of *ponapensis* as "distinctly different" from the other subspecies of *C. inquieta*, describing them as ranging from 6 to 16 cm in depth and "often (attached to) perpendicular cave or crevase walls". Nests of *C. pelewensis*, found in 1958, were described by Brandt (1966) as "very flat structures" with the cup lined with fine grass and moss that were attached on the high ceilings of caves.

Discussion

Medway and Pye (1977) summarized Medway's (1966) and some other data and characterized nests as self-supporting or externally-supported (attached to or supported by rock outcrops or cracks), round or bracket-shaped, whether nest-cement is "moist", "stickly", or "firm", and whether it is "copious" or "sparse" in amount. Some of the terminology used in the descriptions of the types of nests overlap in meaning and the texture and amount of nest-cement may also depend upon the dryness of the season (Tarburton 1988) as well as the age of the nest when described. Medway (1969:58) commented that the nest-cement of many members of *Collocalia* "hardens on exposure to the air ..." and Wells (1975) reported that the nest-cement of what he identified as *C. vanikorensis* became hard when removed from the cave. *C. spodiopygia* hardened with age but became soft with increases in humidity and surface moisture at the nest site.

Descriptions on nest support are also subject to interpretation; nests described as attached to the ceilings of caves (e. g., Jenkins 1983) implies that the nests are self-supported. However, Engbring (in litt.) stated that most nests of the swiftlet in Micronesia are externally-supported, and that the kind of support could be a function of environment rather than an indication of taxonomic affinity. I concur.

Nest shape, although a character in Medway (1966), was excluded for *C. vanikorensis* (sensu Medway 1975) and two other taxa of the 15 listed by Medway and Pye (1977). According to his earlier paper (Medway 1966) the nests are somewhat rounded but tending to be bracket-shaped in *C. vanikorensis*, are rounded in *C. bartschi*, and are "distinctly rounded, (and) suppressed bracket-shaped" to "more rounded" in *C. inquieta*. The shape of the nest of *C. bartschi* was based on two museum specimens, one (USNM) of which is presently too damaged to determine its shape. Brandt (1962), cited by Medway (1966), reported both bracket-shaped and rounded nests in *C. inquieta ponapensis*.

Salomonsen (1983) discussed briefly the variation of nest types among some species (sensu Medway) and similarity of nest types between different species. He concluded that, although information on the type of nest is useful, heavy reliance on nest type for classification of cave swiftlets should be used with caution. I concur. The characters used in the descriptions of nests of *C. vanikorensis* (sensu Medway 1975) include conflicting data; not all populations assigned to *C. vanikorensis* have similar nests. Tarburton (1986) found variation in characters and incorrect localities reported by Medway (1966) of some nests of *C. spodiopygia*. Nests, including the amount of nest-cement, may vary geographically and probably individually in Micronesia. Until standardized and detailed data on nests and nest sites (e. g., humidity) are available I recommend identifying the Micronesian birds on the basis of their morphology.

Biological barriers between the geographically isolated Micronesian populations and *C. vanikorensis* (sensu Salomonsen 1983), if any, are unknown. However, the shared morphological characters of some of the Micronesian populations differ from one another and *C. vanikorensis* (Table 3). Because of these differences I follow Devillers (1977), Owen (1977), and Salomonsen (1983) in recognizing *C. inquieta* as a separate species. I reject the merger of *C. bartschi* with *pelewensis* as a subspecies (Salomonsen 1983) because of their morphological differences. *Collocalia bartschi* likewise differs from *C. vanikorensis*, and is more similar to *C. inquieta*.

Conclusions

The population status of *Collocalia* in Micronesia and Hawaii, based principally on the most current information is:

Collocalia bartschi. Marshall (1949) reported the species as abundant on Saipan and Guam, and flocks on Tinian in mid-October 1945 but none there in mid-November. Breeding on Tinian is not documented. No birds were seen on there in 1976 (Pratt *et al.* 1979) and 1979 (Jenkins and Aguon 1981). Ralph and Sakai (1979) listed the species as common on Saipan. The species was considered abundant by Marshall (1949) and Hartin (1961), and common at one locality there in 1965 (Tubb 1966). Jenkins (1983) considered the population of Guam as one of the rarest native species. Pratt *et al.* (1987) listed swiftlets as uncommon on Tinian, Agiguan, and Saipan, extirpated from Rota, and nearly so on Guam. Birds from Guam were introduced to Oahu, Hawaii, in 1962 (Woodside 1970, Berger 1981). A dozen pairs nested in the central interior in Halava Valley, Oahu, Hawaii, in 1989 (Engbring, pers. comm.).

Collocalia inquieta. Although not observed on Moen Island, Truk Atoll (Baker 1951), Brandt (1962) stated that "it is now one of the commoner birds, of the atoll and is widely distributed among the high islands". Ralph and Sakai (1979) listed the species as abundant on Truck and common on Pohnpei. Population estimates in 1983-84 from unpublished data (J. Engbring *et al.*) are: Kosrae, 27,900; Pohnpei, 29,800; Truk, 25,800.

Peters (1945), Baker (1951) and others included Yap in the range of *C. inquieta ponapensis*. This is based on a sight record of an alleged small swift which Hartlaub and Finsch (1872:93) listed as "*Collocalia*, sp. but was reported as *C.* "*vanikorensis*" by Wiglesworth (1891:353). Pyle and Engbring (1985) reported that this is the only record of the cave swiflet on Yap and doubt its authenticity.

Collocalia pelewensis. Marshall (1949) reported the species to be abundant. Pratt *et al.* (1987) reported absent on Angaur Island. The species is common to abundant on all larger islands from Babeldoab to Peleliu (Engbring 1988), including Ngerukewid (= Ngerukeuid) Islands wildlife Preserve (Wiles and Conry 1990).

Acknowledgements - I thank Robert W. Dickerman for arranging the loan of specimens from the American Museum of Natural History. I also thank J. Engbring, F. L. Ramsey, and V. J. Wildman for use of their population estimates, and J. Reichel for information on nests. I am grateful to J. Engbring for his helpful comments and suggestions on nesting. S. Somadikarta read an earlier version of the manuscript. I thank R. C. Banks, R. B. Clapp, C. T. Collins, J. Engbring, G. R. Graves, J. T. Marshall, S. L. Olson; H. D. Pratt, and M. K. Tarburton reading the manuscript.

Riassunto - Le Collocalie delle isole Mariana, Caroline e Palau costruiscono differenti tipi di nido e differiscono morfologicamente tra di loro e da *Collocalia vanikorensis*.
Le popolazioni delle tre isole sono dunque considerate buone specie, distinte da *C. vanikorensis* e denominate: *bartschi*, *inquieta* e *pelewensis*.

References

American Ornithologists' Union 1983. Check-list of North American birds. Sixth edition. *American Ornithologists' Union. Lawrence, Kansas.*

Beker R. H. 1951. The avifauna of Micronesia, its origin, evolution, and distribution. *Univ. Kansas Publs., Mus. Nat. Hist.* 3:1-359.

Berger A. J. 1981. Hawaiian birdlife. Second ed. *Univ. Hawaii Press, Honolulu.*

Brandt J. H. 1962. Nests and eggs of the birds of the Truck Islands. *Condor* 64:416-437.

Brandt J. H. 1966. Nesting notes on the Collocalia of Micronesia and pennisular (sic) Thailand. *Oologist's Record* 40:61-68.

Crouther M. M. 1983. Observations on White-rumped Swiftlets breeding at Finch Hatton Gorge 1981-82. *Australian Bird Watcher* 10:1-11.

Devillers P. 1977. Projet de nomenclature Française des oiseaux du monde 4. Musophagidés aux Colidés. *Gerf.* 67:337-365.

Dickinson E. C. 1989. A review of larger Philippine swiftlets of the genus *Collocalia. Forktail* 4:19-53.

Engbring J. 1988. Field guide to the birds of Palau. *Conservation Office, Koror, Palau.*

Hartlaub G. and finsch O. 1872. On a fourth collection of birds from the Pelew and Mackenzie islands. *Proc. Zool. Soc. London* 1872:87-114.

Holyoak D. T. and Thibault J.-C. 1978. Notes on the biology and systematics of Polynesian swiftlets. *Bull. British Ornithol. Cl.* 98:59-65.

Hartin M. H. 1961. Birds of Guam, observations from July to Nov. 1960. *'Elepaio* 22:34-38.

Jenkins J. M. 1983. The native forest birds of Guam. American Ornithol. Union, *Ornithol. Monogr.* 31:1-61.

Jenkins J. M. and C. F. Aguon. 1981. Status of candidate endangered bird species of Saipan, Tinian, and Rota of the Mariana Islands. *Micronesica* 17:184-186.

Marle J. G. and van Voous K. H. 1988. The birds of Sumatra. *British Ornithologists' Union Check-list* No. 10.

Marshall J. T. 1949. The endemic avifauna of Sipan, Tinian, Guam and Palau. *Condor* 51:200-221.

Mayr E. 1937. Birds collected during the Whitney South Sea Ewpedition. 33. Notes on New Guinea birds. 1 *American Mus. Novitates* 915:1-19.

Mayr E. 1945. Birds of the southwest Pacific. *Macmillan, Co., New York.*

Medway Lord 1961. The identity of *Collocalia fuciphaga* (Thunberg). *Ibis* 103a:625-626.

Medway Lord. 1966. Field characters as a guide to the specific relations of swiftlets. *Proc. Linnean Soc. London* 177:151-172.

Medway Lord 1969. Studies on the biology of the edible-nest swiftlet of south-east Asia. *Malay Nat. Journ* 22:57-63.

Medway Lord 1975. The nest of *Collocalia v. vanikorensis*, and taxonomic implications. *Emu* 75:154-155.

Medway Lord and Pye J. D. 1977. Echolocation and the systematics of swiftlets. Pp. 225-238 In: B. Stonehouse and C. Perrins, editors. Evolutionary Ecology. *Univ. Park Press, Baltimore*, pp. 225-238.

Owen R. P. 1977. New bird records for Micronesia an major island groups in Micronesia. *Micronesica* 13:57-63.

Peters J. L. 1940. Check-list of birds of the world. Vol. 4. *Harvard Univ. Press, Cambridge.*

Pratt H. D., Bruner P. L. and Berrett D. G. 1979. America's unkown avifauna: the birds of the Mariana Islands. *American Birds* 33:227-235.

Pratt H. D., Bruner P. L. and Berrett D. G. 1987. A field guide to the birds of Hawaii and the tropical Pacific. *Princeton Univ. Press, Princeton.*

Pratt H. D., Engbring J., Bruner P. L. and Berrett D. G. 1980. Notes on the taxonomy, natural history, and status of the resident birds of Palau. *Condor* 82:117-131.

Pyle P. and Engbring J. 1985. Checklist of the birds of Micronesia. *'Elepaio* 45:57-68.

Ralph C. J. and Sakai H. F. 1979. Forest bird and fruit bat populations and their conservation in Micronesia: notes on a survey. *'Elepaio* 40:20-26.

Salomonsen F. 1983. Revision of the Melanesian swiftlets (Apodes, Aves) and their conspecific forms in the Indo-Australian and Polynesian region. *Biol. Skr. Dan. Vid. Selsk.* 23:1-112.

Sibley C. G. and Monroe Jr B. L. 1990. Distribution and taxonomy of birds of the world. *Yale Univ. Press, New Haven.*

Tarburton M. K. 1986. Breeding of the White-rumped Swiftlets in Fiji. *Emu* 86:214-227.

Tarburton M. K. 1988. Breeding biology of the White-rumped Swiftlet at Chillagoe. *Emu* 88:202-209.

Tubb J. A. 1966. Notes on birds of Guam. *Nat. Hist. Bull. Siam Soc.* 21:135-138.

Wells D. R. 1975. The moss-nest swiftlet *Collocalia vanikorensis* Quoy and Gaimard in Sumatra. *Ardea* 63:148-151.

Wiglesworth L. W. 1892. Aves Polynesiae. A catalogue of the birds of the Polynesian subregion. Abhandl. Berichte Königl. Zool. Anthro.-Ethnogr. *Mus. Dresden* 1890/90. N. 6.

Wiles G. J. and Conry P. J. 1990. Terrestrial vertebrates of the Ngerukewid Islands Wildlife Preserve, Palau Islands. *Micronesica* 23:41-66.

Woodside D. H. 1970. Edible-nest swiftlet. *'Elapaio* 31:28.

White C. M. N. and Bruce M. D. 1986. The birds of Wallacea. *British Ornithol. Union Check-list* N. 7.

Avocetta N° 17: 107-110 (1993)

Genetic divergence between Pallid and Common Swifts

ETTORE RANDI and GIOVANNI BOANO

Istituto Nazionale per la Fauna Selvatica,
via Cà Fornacetta 9 - 40064 Ozzano dell'Emilia (BO), Italy.
Museo Civico di Storia Naturale, Carmagnola (TO).
Present address: I.P.L.A., Corso Casale 476 - Torino, Italy.

Abstract We have estimated the average mitochondrial DNA nucleotide divergence between Common and Pallid Swift (*Apus apus* and *A. pallidus*) using the restriction fragment technique. These two species share 63% restriction fragments, which corresponds to about 2% sequence divergence. The study of mitochondrial DNA sequence divergence may be useful to resolve the unclear phylogenetic relationships among many closely related species of swifts.

Introduction

The swifts (Apodidae and Hemiprocnidae) form a very distinct group of a birds with purely superficial resemblances to the swallows (Passeriformes, Hirundinidae). The swifts are usually grouped with the hummingbirds (Trochilidae) in the Order Apodiformes. The recent systematic revision of birds by Sibley and Alquist (1990) supported these affinities, although with a different ranking, placing the swifts and hummingbirds as separate orders (Apodiformes and Trochiliformes) of the superorder Apodimorphae. These Author's use of DNA-DNA hybridization distances suggested an ancient divergence between swifts and hummingbirds possibly dating back to the late Cretaceous.

The 97 species of typical swifts (plus 4 species of crested swifts, *Hemiprocne*) recognized by Sibley and Monroe (1990), are widely distributed in tropical and temperate regions of the world. As a possible consequence of their highly specialized way of life (they are all aerial insect-feeders), swifts show very uniform body structures and low degree of intergeneric species divergence in plumage colors and patterns. Mayr (1970:43) appropriately considered the 12 species of cave swiftlets (*Collocalia*) of the East Indies to be the largest and most morphologically uniform group of sibling species among birds. In a review of the genus *Apus*, Lack (1956) stressed the remarkable difficulty in their classification where differences among species are limited to shades of the dark plumage (varying from brown to sooty or glossy black), the presence or absence of a white rump, body size variations and different wing formulae. Moreover, as some subspecies may differ as markedly as full species, their correct species level classification is, therefore, extremely difficult.

The Common swift (*Apus apus* Linnaeus, 1758) and Pallid swifts (*A. pallidus* Shelley, 1855) are currently considered good biological species, on the basis of a spectrum of characters. The evidence includes morphological characters, egg-shell structure, breeding and migratory habits, voice and assortative mating when in close sympatry (Heim de Balsac 1950, Lack 1956, Boano 1979, Cramp 1985, Malacarne *et al.* 1989). Nevertheless, these two species seem to be closely related, as revealed by the original description of the west Mediterranean Pallid swift (*Apus pallidus brehmorum* Hartert, 1901), in which it was considered a subspecies of *Apus apus* (Peters 1940).

In this paper we estimate the degree of genetic divergence between the Common and Pallid swifts using restriction-fragment length polymorphism of mitochondrial DNA (mtDNA). We aimed to gain insight about their species status, and to apply a method which could be useful to analyse the complex evolutionary relationships of swifts and particularly within the genus *Apus*.

Avian subspecies, or closely related species, usually show low degrees of genetic divergence at the biochemical level (Avise and Aquadro 1982). Genetic distances computed using allozyme electrophoresis are often close to zero, and thus are of little utility in reconstructing phylogenetic relationships among closely related bird species.

Accepted 7 December, 1993

The mitochondrial genome (mtDNA) is a circular DNA molecule approximately 16-17 kb long. It is maternally inherited, accumulates point mutations at rate 5 to 10 times higher than average nuclear DNA sequences, and behaves as a haploid gene without recombination (Wilson *et al.* 1985). Therefore, mtDNA is the molecule of choice for studying genetic divergence and maternal phylogenetic relationships among conspecific populations or closely related species (Ball and Avise 1992, Avise and Zink 1988). In this paper we report preliminary results on mt DNA sequence divergence between Pallid and Common swifts, obtained by mtDNA restrictionfragment analysis.

Methods

Two specimens of Pallid Swifts and two Common Swifts were collected during the breeding season in 1989 near Torino (Piemonte, Italy). Mitochondrial DNA was extracted from liver and heart tissues following a modified alkaline SDS method (Csaikl and Csaikl 1988). Aliquots of mtDNA from each sample were separately digested with a set of 10 restriction endonucleases (Table 1). Fragments were resolved through 1.0% agarose gel electrophoresis in TBE buffer, and Southern blotted overnight on nylon filters. Individual restriction-

Table 1 - Restriction endonucleases used to digest mt DNA of Pallid and Common Swifts, number of restriction fragments scored in the Pallid (nP) and Common (nC) Swifts, number of shared fragments (nPC), estimated percent shared fragments (F) and nucleotide substitutions (D).

Restriction endonucleases	nP	nC	nPC
Hind III	3	3	3
Eco RV	2	1	0
Nde I	2	1	0
Pst I	2	2	2
Hinf I	4	4	4
Hpa I	2	3	1
Dpn I	1	1	1
Sca I	1	2	0
Bgl II	2	2	2
Eco RI	1	2	0

F = 0.63
D = 0.02

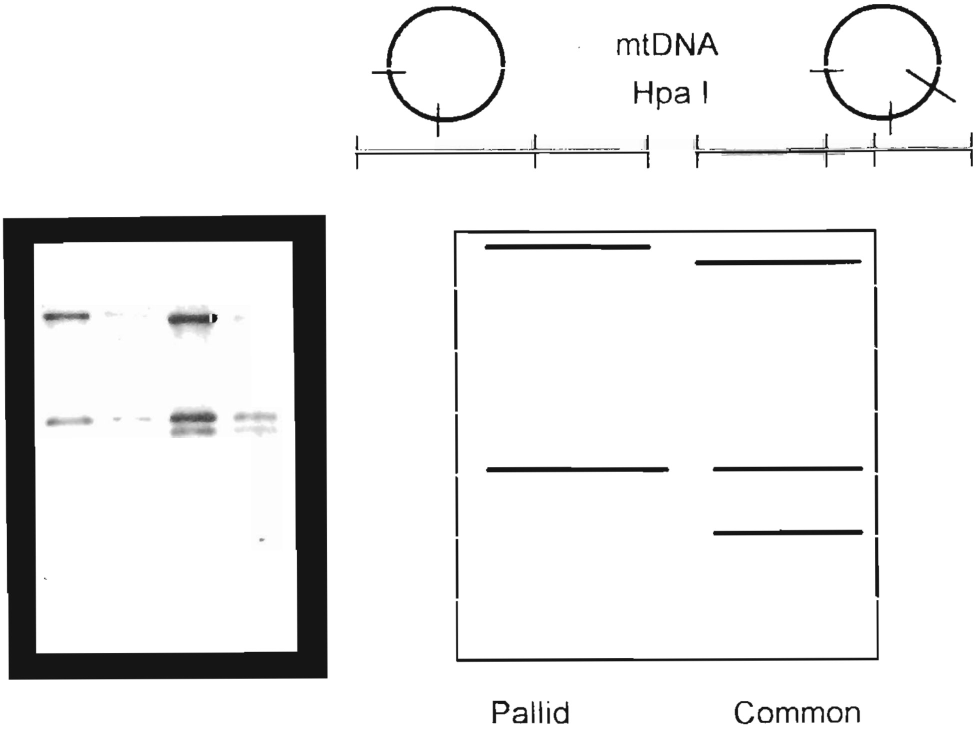


Figure 1 - Digestion of swifts' mtDNA with restriction endonuclease Hpa I. In the Pallid Swifts there are 2 fragments due to the presence of 2 restriction sites. In the Common Swifts there are 3 fragments due to a third restriction site in their mtDNAs. This pattern can be interpreted as a gain or loss of a single restriction site due to a point mutation which creates or destroys the nucleotide sequence GTTAAC recognized by Hpa I.

fragment patterns were scored through hybridization with a cloned entire mouse mtDNA probe. The probe was labelled with alkaline phosphatase and revealed using the AMPPD chemioluminescent method. Autoradiographs on Kodak X-AR films were obtained after 1-3 hours exposure.

Restriction-fragment patterns were scored and the number of fragments were recorded (Table 1)

Genetic distances between species were computed using the method of Nei and Li (1979), which estimates the proportion of shared fragments between two species by the formula:

$F = 2nxy/(nx + ny)$

where nx and ny are the total number of fragments in species x and y, and nxy is the number of shared fragments. The F values can be used to estimate D, the average number of nucleotide substitutions per site for the two species, following the method of Upholt (1977).

Results

Fragment patterns between the two swift species differ for 5 of the 10 enzymes (50%) (Table 1), and differences are always explained by gain or loss of single restriction sites following point mutations (Figure 1). The two samples for each species were identical.

The percent of shared fragments is 63%, corresponding to about 2% sequence divergence between the Pallid and Common swift. Since the average vertebrate mtDNA rate of divergence is 2% per million years (Wilson et al. 1985), we can infer that the divergence between these swifts may be about 1 million years old.

Discussion

We have estimated mtDNA sequence divergence between the Pallid and Common Swifts, two species which are morphologically very similar, and difficult to distinguish in the field or as museum specimens (Boano and Cucco 1989). Nevertheless, these two species show divergent mtDNA sequences, which indicate independent evolution for about 1 million years.

Conspecific bird populations usually have low mtDNA sequence divergence, ranging from 0.0 to 1.0% (Ball and Avise 1992); some avian sibling species also have D values lower than 1% (Avise and Zink 1988). Our mtDNA findings indicate that the Pallid and Common Swifts belong to two anciently separated evolutionary lineages. Their conservative morphology could be the consequence of low rates of phenotypic evolution or, perhaps more likely, of convergence following adaptive selection to very similar habitat and life histories.

In this study we have used small sample sizes, both in birds and in restriction enzymes, to assay mtDNA variation. Therefore, our results need to be confirmed in future studies. In particular, it will be wise to search for intraspecific mtDNA polymorphisms which would affect genetic distances. In addition to the restriction fragment method, it is now possible to sequence mtDNA using PCR (Saiki et al. 1988). This will provide more information on the molecular evolution of swifts. An additional advantage of PCR is the small amount of DNA required (Ellegren 1991), allowing for extensive but undestructive sampling. This approach may be usefully extended to other species (as the Alpine Swift (*Apus melba* Linnaeus, 1758), and particulary to the several medium-sized, black or brown with whitish throat, Afrotropical swifts, whose systematics is still debated. Sibley and Monroe (1990), partially following Fry *et al.* (1988), attribued the "brown" Afrotropical swifts to two groups, with *Apus niansae* Reichenow (1887) included in the superspecies *Apus apus,* and *Apus barbatus* Sclater (1865), *Apus berliozi* Ripley (1965), *Apus bradfieldi* Roberts (1926) and *Apus balstoni* Barlett (1880) included in the superspecies *Apus pallidus*. In a contrary opinion, *Apus barbatus* is considered conspecific with *Apus apus*, or possibly more closely related to *Apus alexandri* Hartert (1901) (Fry et al. 1988:212).

Reconstruction of molecular phylogenetic relationships within the genus *Apus* using mtDNA sequence divergence could be effective in resolving problems such as the example above, and improving our understanding of swift evolution.

Riassunto - Si è stimata la divergenza media del DNA mitocondriale di Rondoni comuni e Rondoni pallidi (*Apus apus* e *A. pallidus*) utilizzando la tecnica di restrizione dei frammenti. Le due specie hanno in comune il 63% dei frammenti di restrizione, la qual cosa corrisponde a circa il 2% di divergenza nella sequenza. Lo studio del DNA mitocondriale può essere utile per risolvere relazioni filogenetiche poco chiare tra specie di rondoni molto simili.

References

Avise J. C. and Aquadro C. F. 1982. A comparative summary of genetic distances in the vertebrates. *Evol. Biol.* 15: 151-185.

Avise J. C. and Zink R. M. 1988. Molecular genetic divergence between avian sibling species: King and Clapper rails, Long-billed and Short-billed dowitchers, Boat-tailed and Great-tailed grackles, and Tufted and Black-crested titmice. *Auk* 105: 516-528.

Ball M. R. and Avise J. C. 1992. Mitochondrial DNA phylogeographic differentiation among avian populations and the evolutionary significance of subspecies. *Auk* 109: 626-636.

Boano G. 1979. Il Rondone pallido *Apus pallidus* nidifica in Piemonte. *Riv. Ital. Orn.* 49: 1-23.

Boano G. and Cucco M. 1989. Breeding biology of the Pallid swift (*Apus pallidus*) in North-Western Italy. *Gerfault* 79: 133-148.

Cramp S. (ed.) 1985. The Birds of the Western Palearctic. Vol IV. *Oxford University Press, Oxford.*

Csaikl U. and Csaikl F. 1988. Speeding-up mitochondrial DNA preparation by a modified alkaline SDS method. *J. Biochem. Biophis. Meth.* 17: 203-206.

Ellegren H. 1991. DNA typing of museum birds. *Nature* 354: 113.

Fry C. H., Keith S. and Urban E. K. 1988. The Birds of Africa. Vol. III. *Academic Press, London.*

Heim de Balsac H. 1950. Les dates de migration et de reprodution du martinet pale en Afrique du Nord. Tests ecologiques de differentiation specifiques. *Alauda* 17-18: 108-112.

Lack D. 1956. The species of *Apus*. *Ibis* 98: 34-62.

Malacarne G., Palomba I., Griffa M., Castellano S. and Cucco M. 1989. Quantitative analysis of the differences in the vocalization of the Common Swift *Apus apus* and Pallid Swift *A. pallidus*. Avocetta 13: 1-6.

Mayr E. 1970. L'evoluzione delle specie animali. *Boringheri, Torino.*

Nei M. and Li W. 1979. Mathematical model for studying genetic variation in terms of restriction endonucleases. *Proc. Natl. Acad. Sci. (USA)* 76: 5269-5273.

Peters J. L. 1940. Birds of the world. Vol. IV. *Harvard University Press, Harward.*

Saiki R. K., Gelfand D. H., Stoffel S., Scharf S. J., Higuchi R., Horn G. T., Mullis K. B. and Herlich H. K. 1988. Primer-directed enzymatic amplification of DNA with a thermostable DNA polymerase. *Science* 239: 487-491.

Sibley C. G. and Alquist J. E. 1990. Phylogeny and Classification of Birds. *Yale University Press, New Haven and London.*

Sibley C. G. and Monroe B. L. Jr. 1990. Distribution and Taxonomy of Birds of the World. *Yale University Press, New Haven and London.*

Upholt W. B. 1977. Estimation of DNA sequence divergence from comparison of restriction endonuclease digests. *Nucleic Acid Res.* 4: 1257-1265.

Wilson A.C., Cann R. L., Carr S. M., George M., Gyllensten U.B., Helm-Bychowski K. M., Higuchi R. G., Palumbi S.R., Prager E. M., Sage R. d. and Stoneking M.1985. Mitochondrial DNA and two perspectives on evolutionary genetics. *Biol. J. Linn. Soc.* 26: 375-400.

Avocetta N° 17: 111-115 (1993)

A preliminary note on the chromosome complement of the House Swift, *Apus affinis*

N. Andayani, D. P. Astuti and S. Somadikarta

Department of Biology, University of Indonesia - Depok 16424 Indonesia.

Abstract The karyotype of *Apus affinis* presented by Bhunya and Mohanty (1987 showed a remarkable difference of chromosome number (78) compared to the other three swift species studied so far 62, 64 and 62 respectively). Re-examining its chromosome number revealed a discordant result, with only 68 chromosomes. A comparison of the karyotype of *A. affinis* with that of *A. apus* shows a great difference in the number of macro- and microchromosomes, despite a morphological resemblance of macrochromosomes 1 to 6. The possible mechanism which can account for the addition of chromosome number of *A. affinis* is discussed.

Introduction

The use of morphological characters alone in a homogenous group of birds is often not sufficient to clarify taxonomic relationships between species. Given the utility of karyotypic data in determining relationships amongst species of mammals (Searle *et al.* 1989, Fredga *et al.* 1980), very little attention has been given to this technique as a taxanomic tool in bird systematics. Up to 1990, only 800 species of birds have been karyotyped and even fewer have been analyzed with differential banding techniques (Christidis 1990).

The lack of complete descriptions of more avian karyotypes is largely due to the difficulties in obtaining good chromosome preparations (Belterman and De Boer 1984; Christidis 1985; Shields 1987). Moreover, the organization of avian karyotypes makes detailed analysis difficult. Most birds have high diploid chromosome numbers ranging from 60 to 126 and the majority of these chromosomes are minute and obscure (Hammar 1970, De Boer and Sinoo 1984).

The diverse opinion on karyotypic similarity combined with the small size of the chromosomes has inevitably further discouraged works on avian cytotaxonomy. Swifts (Apodidae) are one of the least studied families in avian cytogenetics. Of about 84 species belonging to this family (Howard and Moore 1980), only 4 species have been karyotyped. Those species are reported to have different diploid numbers of chromosomes: *A. affinis* with 2n=78 (Bhunya and Mohanty 1987), *A. pacificus* and *Hirundapus caudacutus* have 2n=62 and 2n=64 respectively (Bian *et al.* 1980), while *A. apus* has 2n=62 (Andayani 1990). Therefore, avian karyotypes are not as conservative as previously reported and it is already evident that species of the Apodidae show substantial karyotypic variation.

The karyotype of *A. affinis* reported by Bhunya and Mohanty (1987) differs remarkably from the other swift species. This report suggested the species has 78 chromosomes, which can be easily divided into 7 pairs of macro- and 32 pairs of microchromosomes. On the contrary, the other three swift species are reported to have only 62-64 chromosomes with 6 pairs of macrochromosomes. Such a great difference in chromosome number in congeneric species has not been reported previously in birds. Therefore, the question arises whether several fissions have actually occured in *A. affinis* or if another explanation should be put forward to account for this unusual karyotypic variation.

This study was carried out to re-examine the chromosome number of *A. affinis* and to determine possible mechanisms underlying the additional number of homologues.

Methods

Swifts were collected from nests found in Senayan, Jakarta. Birds used in this study were both young and adult individuals. Somatic metaphase chromosomes were prepared using an *in vitro* bone marrow procedure described by Fredga (1987). Bone marrow cells from both femur and tibia were incubated in

---

Accepted 30 December 1993

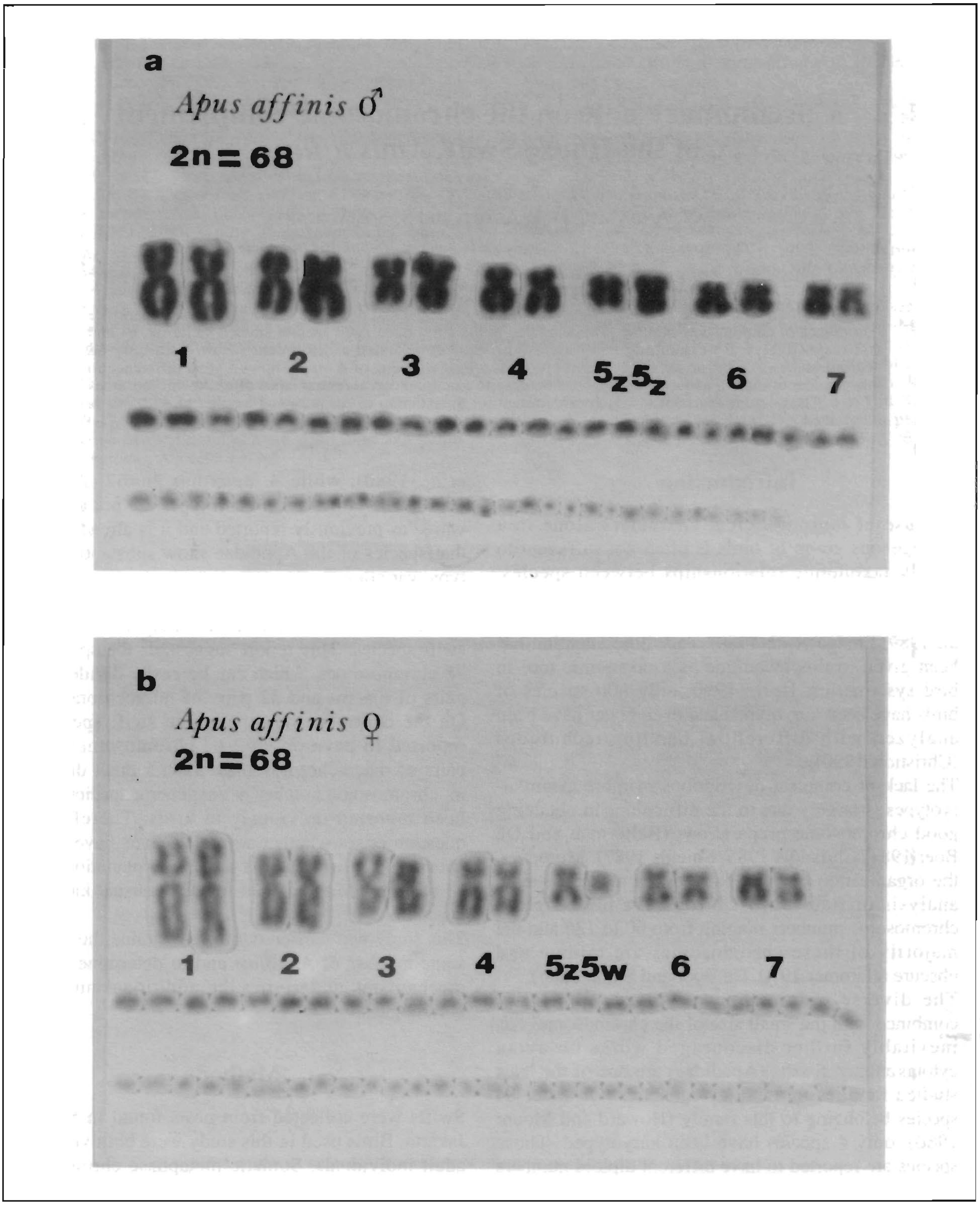


Figura 1. Karyotype of *A. affinis*, a: male; b: female

RPMI 1640 medium (Flow laboratories) supplemented with 15% Fetal Bovine Serum (FBS). To each 5 ml of media-cell suspension, 0.1 ml colchicine (0.01%) was added. This was then incubated at 37° for 30-40 min. The cells were treated in hypotonic solution (0.4% Kcl) for 15-30 min, then fixed in three changes of 3:1 methanol-glacial acetic acid. Splash preparations were made by dropping two separate drops of the cell suspension onto a clean and dry slide from a height of 10-30 cm. The slides then were air dried and stained for 8 min in 5% of Giemsa solution.

Favourable cells were photographed with a NIKON HFX camera mounted on a NIKON LABOPHOT microscope at a magnification of 500x. Kodak Technical Pan 135 film was used and developed in KODAK PRO B/W for 7 min.

An idiogram of *A. affinis* was constructed based on measurements of 10 selected pictures. Only 7 chromosome pairs (6 pairs of autosomes and the ZW chromosome) were measured individually. To simplify the measurements of the rest of the chromosome complement, which were minute and indistinct, measurements were done on the first several chromosomes which could be seen quite clearly and a few last ones. The chromosome length of microchromosome components was then determined by averaging those values.

The chromosome designation followed the nomenclature proposed by Levan *et al.* (1964) and arranged according to decreasing length.

Results

The diploid chromosome number is 68. The karyotype is shown in Figure 1 and the idiogram in Figure 2. The results of the chromosome measurements are presented in Table 1. With respect to the position of the centromere (centromeric index), each chromosome is included in one of classes m, sm, st, and t. (Levan *et al.* 1964). The range of relative length is 6.63 to 20.33.

The karyotype consists of 7 pairs of macrochromosomes, including the Z, and 27 pairs of microchromosomes. The first three autosome pairs are comprised of m chromosomes, while pairs 4, 6, and 7 are sm. All microchromosomes are made up of t elements. As expected, females have ZW sex chromosomes, males ZZ. The Z chromosome is an m

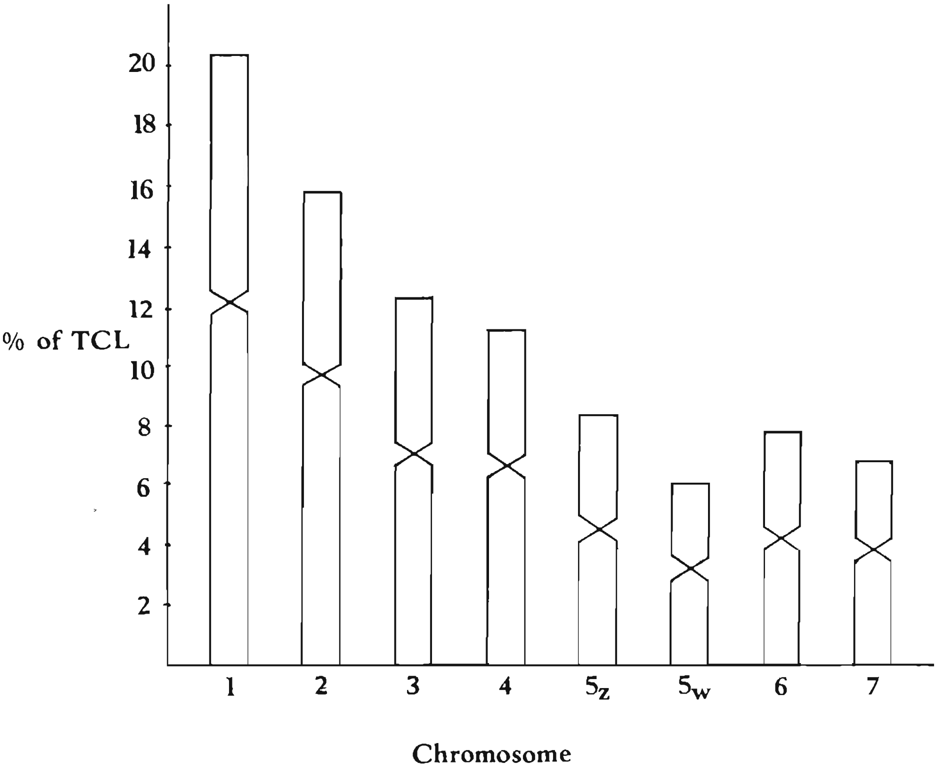


Figura 2. Idiogram of *A. affinis*; unit of ordinate per cent of total haploid male chromosome length.

Table 1. Chromosome measurement of *A. affinis*. Mean of 5 female and 5 male cells.

Chromosome	Chromosome designation[1]	Relative length % of male haploid set				Centromeric index[2]	
		p mean	q mean	p+q mean	se	mean	se
1	m	8.09	12.24	20.33	1.52	39.42	3.98
2	m	6.14	9.71	15.85	1.18	39.58	4.39
3	m	5.32	7.01	12.33	0.84	43.28	4.22
4	sm	4.61	6.61	11.22	0.58	31.19	5.65
5_Z	m	3.88	4.5	8.38	0.96	46.71	3.07
5_W	m	2.80	3.24	6.04	2.84	47.43	2.56
6	sm	3.49	4.24	7.73	1.22	34.75	4.16
7	sm	2.80	3.83	6.63	1.34	32.16	3.84

[1]:The nomenclature symbols recommended by Levan *et al.* (1964)

[2]:The centromeric index, i = p/(p+q)·100; p= short arm of chromosome, q= long arm of chromosome (Fredga, 1972)

type and fifth in size, the W is also identified as an m with the size of a microchromosome. All macrochromosomes are relatively easy to identify on the basis of length and centromeric index, while the remaining microchromosomes comprise elements of gradually decreasing size which are impossible to distinguish individually.

Discussion

The karyotype of *A. affinis* studied previously by Bhunya and Mohanty (1987) showed a remarkable difference when compared to other swift species. The diploid number is 78 with 7 pairs of macrochromosomes which can be easily distinguished from the microchromosomes by their size.

Karyotypic description of *A. affinis* in this study revealed a discordant result from that of Bhunya and Mohanty (1987). In this study the diploid number of *A. affinis* is 68 with 7 pairs of macrochromosomes and 27 pairs of microchromosome. Despite the great difference in the diploid chromosome number, the macrochromosome complements show a morphological resemblance to the karyotypic description reported later by Mohanty (1987).

The discrepancies of chromosome number of *A. affinis* from the two studies might be due to errors in determining microchromosome numbers in the former study. Microchromosome are difficult to count in a light microscope and can easily escape from one metaphase plate and join an other during preparation, resulting in higher chromosome counts. Moreover small spots of dye can be misjudged as microchromosomes. The karyotype of *A. affinis* is nearly identical to that of *A. apus* (Andayani 1990), except that the later species has a diploid chromosome number of 62 and lacks the sm pair of macrochromosome 7. Nevertheless, the difference in chromosome number cannot be easily explained by proposing simple Robertsonian translocations.

Tegelstrom and Ryttman (1981) have shown that there is a negative correlation between the number of macro and microchromosome in birds. If the number of macrochromosome increases, then the number of microchromosome will decrease. However, this rule is not applicable to *A. affinis* in which both macro- and microchromosomes number is increased.

The possible explanation to account for such karyotypic variation in the two species is that the 7th macrochromosome pair of *A. affinis* was derived from fusion of the two largest microchromosomes of *A. apus*. This was then followed by fissions of various microchromosomes. This suggestion is supported by the difference in the size of macro- and microchromosomes between the two species. The size of macro- and microchromosomes of *A. affinis* is clearly different, whereas *A. apus* shows a gradual decrease of chromosome size. However, it is difficult to prove that fission of microchromosomes has really taken place, since the small size of microchromosomes makes detailed analysis difficult. Nevertheless, it is obvious that more species should be studied before a comprehensive picture of chromosomal diversity of the Apodidae can be established.

Acknowledgments - Our sincere gratitude is due to Professor N. Suhana and his collagues at the Biology Division, Fac. Medical Science, Univ. of Indonesia, especially Dra. Pudjisari, for their excellent guidance in microphotography. We also would like to thank Wisnu Wardhana for helping us with the photography. Farah and Tita have been a great help during the completion of this work, we would like to thank them for it.
This work was supported by grant from The Toray Science Foundation through a cooperation with Institute for Research, University of Indonesia.

Riassunto - Il cariotipo di *Apus affinis* studiato da Bhunya and Mohanty (1987) mostra un numero cromosomico (78) molto più alto rispetto ad altre tre specie di rondoni studiati (62, 64 e 62 rispettivamente). Questo studio invece mostra soltanto 68 cromosomi. La maggior differenza rispetto ad *A. apus* risulta essere il numero di macro e microcromosomi, nonostante la notevole somiglianza dei macro cromosomi da 1 a 6. Si discutono i meccanismi che hanno portato *A. affinis* ad avere cromosomi addizionali.

References

Andayani N. 1990. The karyotype of the common swift *A. apus* (Aves; Apodidae). *Thesis -MSc, Uppsala University.*

Belterman R.H.R. and De Boer L.E.M. 1984. A karyological study of 55 species of birds, including karyotypes of 39 species new to cytology. *Genetica* 65: 39-82.

Bhunya S.P. and Mohanty M.K. 1987. Studies on the karyotypes and bandings of 41 species of indian birds (Aves). *Chrom. Inf. Ser.* 42: 12-15.

Bian X. Li Q. and Zhang H. 1988. Chromosomes atlas of birds. ISBN7-5611-0085-X/Q. 6: 236 p.

Christidis L. 1985. A rapid procedure for obtaining chromosome preparations from birds. *Auk* 102: 892-893.

Christidis L. 1990. Chromosomal repatterning and systematics in the passeriformes (songbirds) . In: Fredga K., Kihlman B. and Bennett M.D. (eds) Chromosomes today. *Unwin Hyman, London*: 279-294.

De Boer L.E.M. and Sinoo R.P. 1984. A karyological study of Accipitridae (Aves: Faconiformes) with karyotypic descriptions of 16 species new to cytology. *Genetica* 65: 89-107.

Fredga K. 1972. Comparative chromosome studies in mongooses (Carnivora, Viveridae): I. Idiograms of 12 species and karyotype evolution in Herpestine. *Hereditas* 71: 1-74.

Fredga K. 1987. Chromosome preparations in the field from mammals long after death. *Stain Technology* 62: 167:171.

Hammar B. 1970. The karyotypes of thirty-one birds. *Hereditas* 65:29-58.

Howard R. and Moore A. 1980. A complete checklist of the birds of the world. *Oxford University Press, Oxford*: vii + 732 p.

Levan A., Fredga and Sandberg A.A. 1964. Nomenclature for centromeric position on chromosomes. *Hereditas* 52: 201-220.

Mohanty K. 1987. Karyological studies of some Indian birds. *Thesis-PhD, Utkal University, India.*

Shields G.F. 1987. Chromosomal variation. In: Cooke F. and Buckley P.A. (eds) Avian genetics. *Academic Press, London*: 79:101.

Tegelstrom H. and Ryttman H. 1981. Chromosomes in birds (Aves): volutionary implications of macro- and microchromosome numbers and lengths. *Hereditas* 94: 255- 233.

Wang H.C. and Fedorrof S. 1972. Banding in human chromosomes treated with trypsin. *Nature New Biol.* 235: 52-53.

Avocetta N° 17: 117-123 (1993)

Patterns of distribution of swifts in the Andes of Ecuador

MANUEL MARIN

Western Foundation of Vertebrate Zoology,
439 Calle San Pablo, Camarillo, California 93010 U.S.A.
Present address: Museum of Natural Science,
Louisiana State University, Baton Rouge, Louisiana 70803 U.S.A

Abstract Trans-Anden elevational (above sea level) and vertical (above ground) patterns of distribution of the resident swifts species in Ecuador were examined. The four types of limits for species distribution along an elevational gradient proposed by Terborgh (1971) and Terborgh and Weske (1975) were assessed as to their effects in swift distribution. 1) "Natural terminus of the environmental gradient" might affect only two species. 2) "Factors in the physical or biological surroundings that change parallel with the gradient" were possibilities for six of 10 species. 3) "Competitive exclusion" was not found in the elevational gradient, but, is likely to operate in partitioning the vertical component. 4) "Vegetational ecotones" did not seem to affect the aerial guild.

Introduction

Little has been written on the distributional patterns of Neotropical birds along elevational gradients. The scant literature (e.g., Terborgh 1971, Terborgh and Weske 1975, Remsen and Cardiff 1990, Remsen and Graves in press) has considered the role of competition in shaping distributional patterns. None of these studies have described the patterns of elevational distribution in the aerial foraging guild, which in the Neotropics includes two families, Apodidae (swifts) and Hirundinidae (swallows and martins), as well as some subgroups such as the nighthawks (Chordeilinae spp. etc.) and some birds of prey (e.g., *Ictinia, Elanoides*). In this paper only the swifts, the core of the guild, will be treated.

Determining the distributional patterns of swifts is complex. Not only are they highly mobile, but they are also morphologically similar and difficult to distinguish in the field. Also, they usually fly fast and erratically, often high above the ground. Therefore, the core of the guild is a group difficult to observe, collect, and identify in the field. Furthermore, the elevational distribution of swifts has two distinct components: a) elevation above sea level, which I will refer to as "elevational", and b) altitude above the ground, which I will call "vertical." Only two studies, Hespenheide (1975) and Waugh and Hails (1983) have described the vertical component of the aerial guild in the tropics. Both studies described foraging interactions and difference among swallows and swifts. In this paper I will primarily present information on the elevational component of swift distribution, but I will also present some preliminary data on the vertical component.

Methods

Data on swift distribution in Ecuador were gathered from 1987-1992, while participating on expeditions to survey bird distribution sponsored by the Western Foundation of Vertebrate Zoology (WFVZ). In total, over 15 months of field work were conducted during the five-year period. Selected stations (presented in Table 1) correspond to some WFVZ camps or often-visited localities, where a large part of the data were obtained in the form of observations and specimens. To supplement these observational data on distributional patterns, a combination of extensive observations at random localities throughout the country, localities from museum specimens, and some published records were added. When the elevation or full locality were lacking for any museum specimen, they were supplemented by information obtained from Paynter and Traylor (1977). In addition, several road surveys on both sides of the Andes were conducted, mostly during the months of May through September, but with some data collected from November through January.

The main objective in this project was to delineate the upper and lower limits of distribution of each species.

Accepted 30 November, 1993

Table 1. Selected working stations in Ecuador and relative abundance of swift species.

LOCALITY; PROVINCE	SPECIES[1] *Str. zonaris*	*Str. rutila*	*Cyp. cherrei*	*Chae. cin.*	*Chae. brach.*	*Chae. spin.*	*Chae. egregia*	*Pan. caye.*	*Tac. squam.*	*Aeron. mont.*
Western Slope										
above Cotocollao (3300 m); Pichincha	C	-	-	-	-	-	-	-	-	-
Las Palmeras (1900); Pichincha	U	C	R	-	-	-	-	-	-	-
near Nanegalito (1500 m); Pichincha	C	C	-	-	-	U	-	R	-	-
Near Piñas (900 m); El Oro[3]	C	R	-	C	U	-	-	R	-	-
Near Vicente Maldonado (600 m); Pichincha	C	R	-	-	-	C	-	U	-	-
La Mana (550 m); Cotopaxi	U	-	-	C	-	U	-	R	-	-
Chindul Mts. (450 m); Manabi	U	U	-	C	-	U	-	-	-	-
Maicito (300 m); Manabi	U	-	-	C	-	-	-	R	-	-
Inter-Anden Valleys										
Tanlahuila (2700 m); Pichincha	R	-	-	-	-	-	-	-	-	C
near Puellaro (2000 m); Pichincha	R	-	-	-	-	-	-	-	-	C
6 Km E Chota (1500 m); Carchi	-	U	-	-	-	-	-	-	-	C
Eastern Slope										
La Virgen (4000 m); Napo	C	-	-	-	-	-	-	-	-	-
NE Archidona (1400 m); Napo	C	U	-	-	-	-	-	-	-	-
Pachicutza (1000 m); Zamora-Chinchipe	C	U	-	C	-	-	U	-	C	-
Tayuntza (600 m); Morona-Santiago	C	U	-	C	-	-	U	R	-	-
near Coca (300 m); Napo	U	-	-	-	C	-	-	U	U	-

[1] *Cypseloides cryptus* was excluded, because of uncertainty in locality.
[2] Relative abundance indicated as: C = common, recorded daily or every other day in moderate to large numbers > 15; U = uncommon, recorded every few days in small numbers < 10; R = rare, few < 5 birds recorded for the area.
[3] Data from Robbins and Ridgely (1990) and personal observation.

Table 2. Swifts species that occur in Ecuador, with clutch size, growth rates, body mass, and foraging stratum.

Species	Clutch size[1]	Growth[2]	Body mass[3] (g)	Vertical foraging[4]
White-collared Swift *Streptoprocne zonaris*	2	Slow	103.7	High
Chestnut-collared Swift *Streptoprocne rutila*	2	Slow	21.3	High*
Spot-fronted Swift *Cypseloides cherriei*	1	Slow	23.2	High
White-chinned Swift *Cypseloides cryptus*	1	Slow	35.2	High
Chimney Swift *Chaetura pelagica*	4	Fast	23.6	Low*
Gray-rumped Swift *Chaetura cinereiventris*	4	Fast(?)	18.6	Low*
Short-tailed Swift *Chaetura brachyura*	3-4	Fast	18.3	Low*
Band-rumped Swift *Chaetura spinicauda*	?	Fast(?)	15.9	Low*
Pale-rumped Swift *Chaetura egregia*	?	Fast(?)	22.6	Low*
White-tipped Swift *Aeronautes montivagus*	?	?	19.6	Low
Lesser Swallow-tailed swift *Panyptila cayennensis*	2-3	?	18.1	High
Fork-tailed Palm-Swift *Tachornis squamata*	3	?	11.7	Low

[1] Summaries in Collins (1968b), Sick (1986) and Marín and Stiles (1992).
[2] Growth (days): Fast = < 40; Slow = > 40 (summary in Marín and Stiles 1992).
[3] Body masses from above citations and Marín *et al.* (1992).
[4] Foraging strata in mixed-species flocks. For simplicity the vertical component was subdivided into high and low (ca. first 15 m above ground or vegetation for low.); (*) = species that might use either stratum, but only primary stratum is given.

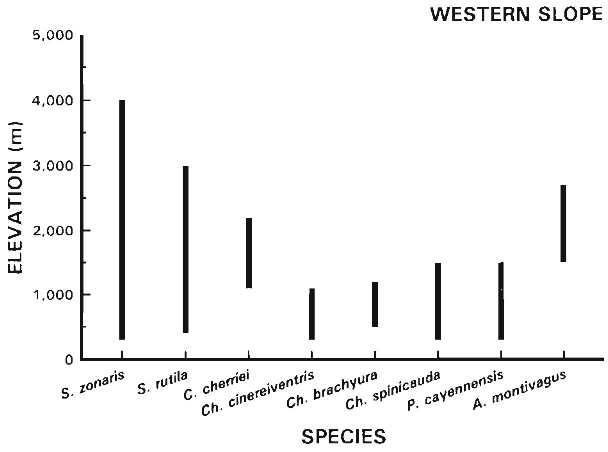


Figure 1. Elevational distribution of swifts in western Ecuador. Although *C. cherriei* is known from only one locality in Ecuador, the upper and lower limite from elsewhere in its range was used here (c.f. Marín and Stiles 1993).

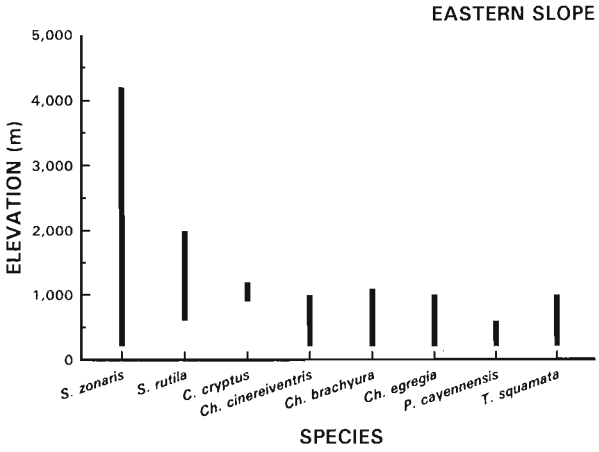


Figure 2. Elevational distribution in eastern Ecuador. (Although the distribution of *C. cryptus* in Ecuador is of uncertain status; see text for basis for its inclusion in this figure).

Consequently, the abundance of each species throughout its elevational distribution was assessed only generally. For some species, especially those with a broad elevational range, some semi-quantitative measures of abundance will be introduced ("common", "uncommon" and "rare"; Table 1).

I encountered many problems with attemping to quantify relative species abundance. Some swifts can easily use the complete altitudinal gradient on a daily basis and move across land barriers that would be difficult, if not impossible, to overcome for many terrestrial birds. Furthermore, some species move extensively along both gradients, elevational and vertical, making independent observations difficult. In a matter of hours they can cover perhaps the entire gradient more than once. Distribution of species in the genus *Streptoprocne* is particularly difficult to quantify because of this; not coincidentally, these species have the broadest distributional range of the species studied (see Figs. 1 and 2). Further complications arise in the vertical component, because most species forage in mixed-species flocks, and some species are difficult to distinguish. Nevertheless, some patterns did emerge, and these can be used for future lines of inquiry.

Ecuador presents an unique opportunity for a trans-Andean distributional survey. The Ecuadorian andes consist of a relatively uniform main chain, located between ca. 1° N and 4° 30'S. Both slopes of the Andes are rather steep, ascending quickly to tree line or above. As a result, access to the highlands on either slope of the Andes is limited. Inter-Andean valleys, usually arid and formed by rivers that flow either east or west, form the division between the eastern and western slopes. The river generally descend gradually through the inter-Andean valleys, but form narrow canyons with steep slopes as they descend through mountain gaps. On both sides of the Andes the gradient ranges from tropical lowland forest to páramo and snow line. Altitudinal divisions used here are: Tropical 0-1200 m; Subtropical 1200-2300 m; Temperate 2300-3100 m; and Páramo 3100-5000 m; inter-Andean valleys occur at 1500-3200 m.

Results

Based on present taxonomy and knowledge of the Ecuadorian avifauna, the country contains 11 species of swifts in six genera (Table 2).

One of these species is a long-distance migrant, from North America, the Chimney Swift (*Chaetura pelagica*). Because of its transient status, this species was exluded from the figures.

Elevational patterns (from sea level): Eight species of swifts were detected on each side of the Andes (Figs. 1 and 2). At no elevation on either side did all eight species overlap. The maximum number of swift species found at a single site at the same time was five, but regularly two-three species per locality were encountered (also cf. Table 1). *Streptoprocne* spp. were abundant throughout the gradient. The White-collared Swift *Streptoprocne zonaris* was found to have the broadest elevational, distribution, from 300-4000 m on the western slope and from 300-4200 m on the eastern slope. This species was almost equally abundant at all elevations, surprisingly, even at 4000 m (e.g., at La Virgen, above Papallacta, prov.

Pichincha). The highest breeding record for the species is from a locality above Quito at 3200 m (Lönnberg and Rendahl 1922). Only one other species, the Chestnut-collared Swift (*S. rutila*) (For the inclusion of this species in *Streptoprocne*, see Marín and Stiles 1992), had as broad an elevational range with its highest breeding record at 2300 m (Kiff et al. 1989); however, it was rather uncommon at high elevations. *Streptoprocne rutila* was more abundant in the mid-elevations of its range, ca. 800-1500 m (Figures 1 and 2).

In contrast, there were very few records for the *Cypseloides* spp. For example, the White-chinned, Swift (*C. cryptus*) might occur on both slopes of the Andes in Ecuador, because there are some specimens from southern and northern Colombia, along the central and western Andes (Eisenmann and Lehmann 1962). However, the only Ecuadorian specimen of *C. cryptus* lacks specific locality data (British Museum Natural History # 8873066, ex-Gould coll.). *Cypseloides cryptus* was placed on the eastern side of the Andes (Fig. 2), based on speculation that the specimen originally identified as the Sooty swift *C. fumigatus* (Hartert 1892), but later shown to be *C. cryptus* (Collins 1968a), came from the Napo region. I suspect thet this specimen was included in a collection from the Napo that J. Gould received in about 1854 and sent to P. L. Sclater at BMNH for identification (Chapman 1926). There are many records for the species north of Ecuador and the type locality for the species is in southeastern Peru (Zimmer 1945), making the presence of *C. cryptus* in eastern Ecuador likely. A second bird reported as *C. fumigatus* by Salvadori and Festa (1900) from eastern Ecuador, Gualaquiza, prov. Morona-Santiago, might also be *C. cryptus*, because many old specimens reported as *C. fumigatus* were actually *C. cryptus* (Zimmer 1945). In other parts of its range *C. cryptus* has been found from sea level to 2000 m (Rogers 1939; Marín and Stiles 1992). Likewise, the Spot-fronted Swift *C. cherriei* is known only from one locality in Ecuador, Las Palmeras (1900m), prov. Pichincha. Elsewhere in its range, it is found in the subtropical belt from 1100 to 2200 m (Marín and Stiles 1993).

The Lesser Swallow-tailed Swift *(Panyptila cayennensis)* was present on both slopes. It was never abundant and was found mainly in small groups of 3-5, or as solitary individuals. On the western slopes I found it in the upper tropical-subtropical range from 300 to 1500 m (Fig. 1), whereas on the eastern slopes it had a norrow range in the tropical zone from 200 to 600 m (Fig. 2). It is likely that the species occurs at higher elevations on the eastern slope, although less abundantly. On both slopes, I found it most common in the 300-500 m range.

The White-tipped Swift (*Aeronautes montivagus*) was found only in the inter-Andean zone, from 1500 to 2700 m (Fig. 1), in valleys dropping to the west, where it was abundant but patchy in distribution. It should also be present in valleys dropping to the eastern slopes; however, I did not encounter it there, and I did not adequately survey most of those valleys. The Fork-tailed Palm-Swift (*Tachornis squamata*), another species with a patchy distribution, was present only on the eastern slope of the Andes in the tropical zone from 200 to 1000 m and was always found associated with palms.

Two *Chaetura* spp., the Gray-rumped Swift (*C.. cinereiventris*) and the Short-tailed swift (*C. brachyura*), were present on both slopes. The former was common on both sides of the Andes, from ca. 200-1000 m (Fig. 1 and 2). However, on the eastern slope it gradually increased in abundance toward the upper part of its range, whereas on the western slope it was gradually more abundant in the lower part of its range. East of the Andes, *C. brachyura* seems to have a slightly broader elevational range than on the western slope. However, on the western slope *C. brachyura* seems to be present only in the south; there are no specimens north of prov. El Oro. Nevertheless, there are some specimens from western Colombia and from the southern end of El Valle del Cauca (specimen at Museo de Zoologia, Universidad del Valle, Cali, Colombia, ex-INCIVA and Lehmann collection). *C. brachyura* ranges on the eastern slope from 200-1100 m (Fig. 2) and was the most abundant species of *Chaetura* in the lower part of its ra-nge (ca. 200-500 m). The Band-rumped Swift (*C. spinicauda*) had the broadest elevational range of any *Chaetura* spp., mainly in the lower subtropical zone from 300-1500 m (Fig. 1); however, it was more abundant in the 450-900 m range. The Pale-rumped Swift (*C. egregia*) replaced *C. spinicauda* on the eastern slope, ranging from 200-1000 m, where it was abundant in the higher portion of its range. *C. pelagica* has been recorded on both sides of the Andes in South America. In Ecuador I have records from 300-1000 m on the eastern slopes and in the inter Andean Valle de Quito at ca. 2500 m. This species is also expected to pass through the western slope, because it has been recorded in coastal or western Colombia, Peru, and Chile (Miller 1962, Koepcke 1964, Araya *et al.* 1972, Plenge 1974), but at present there are no definitive records for western Ecuador.

Vertical patterns (from ground): This is most the complex distributional component of the aerial guild, and a paucity of data prevents a quantitative analysis of vertical diferences. However, Marín and Stiles (1992) suggested one way that non-congeneric swifts might divide their aerial resources. These authors suggested an analogy with seabirds, in which species with large clutch sizes, and thus fast growth rates, should forage closer to the nest (and thus also closer to the ground), whereas species with small clutch sizes, and slower growth rates, should forage farther away from the nest (and thus also higher above the ground). Indeed, *Chaetura* spp., which all have large clutch sizes, do forage nearer to the ground than other swift species (cf. Table 2). For example, in one assemblage of four species on the western slopes (such as at Chindul Mts.; Table 1), vertical stratification was observed when two or more species were present. However, when two or three smaller species (*S. rutila, C. cinereiventris* and *C. spinicauda*) were present, there was no clear division, especially between the two *Chaetura* spp. When all species foraged together at one site, the stratification was fairly distinct. In order decreasing foraging height, it was as follows: *S. zonaris*, *S. rutila*, *C. cinereiventris*, and *C. spinicauda*. An assemblage of five species on the eastern slopes at Pachicutza (Table 1) was organized similarly (decreasing height): *S. zonaris*, *S. rutila*, *C. egregia*, *C. cinereiventris* and *T. squamata*. On both sides of the Andes, the vertical stratification between the *Streptoprocne* and *Chaetura* spp. correlates with clutch-size and growth-rate. Although there are no data on clutch size or growth rate for all *Chaetura* spp., those species in this genus for which data are available all have a large clutch size and a fast growth rate (Table 2). It was difficult to distinguish any clear vertical segregation between *C. egregia* and *C. cinereiventris*, but *C. egregia* seemed to predominate in the upper strata. On the other hand, *T. squamata* has a clutch size smaller or equal to *Chaetura* spp., but is much smaller in body size (Table 2).

In the presence of most species, *Panyptila cayennensis*, with an intermediate clutch size of three eggs, usually foraged in the upper stratum. However, when *P. cayennensis* was in the presence of *S. zonaris* and *Cypseloides* spp., it used a lower stratum. When *P. cayennensis* and *T. squamata* foraged together, *T. squamata* (also with a clutch size of three) used the lower stratum. Also, when *P. cayennensis* foraged with any species of *Chaetura* it used the upper stratum. When *Tachornis squamata* was together with any species of *Chaetura* or *Streptoprocne*, it primarily used the lower stratum. *Aeronautes montivagus* rarely was observed foraging with other swift species. However, most of the time *A. montivagus* foraged in the lower stratum, even in the presence of other species. Although these general patterns of vertical segregation were evident, it must be emphasized that any species foraging in a single-species flock or singly might forage in any or all strata.

Discussion

Terborgh (1971) and Terborgh and Weske (1975) proposed four types of limits for species distribution along an elevational gradient: 1) natural terminus of the environmental gradient, 2) factors in the physical or biological surroundings that change parallel with the gradient, 3) competitive exclusion between congeners, and 4) vegetational ecotones. The natural environmental or vegetational terminus as a distributional limit seems likely for two Ecuadorian swifts. *Tachornis squamata* is found associated primarily with, and thus limited by, palm distribution, mainly that of *Mauritia* spp., on which it depends for nesting sites. *Aeronautes montivagus* is virtually restricted to arid or semiarid habitats, primarily along the inter-Andean valleys. Other species are more flexible in their habitat; as noted earlier *S. zonaris* can be found from the tropical lowlands to the páramo.

Many factors in the physical and biological surroundings change in parallel with the gradient, especially temperature, rainfall, and presumably insect density. Because all resident species of *Chaetura* were found only in the lowlands, it is possible that some physical or biological factor influences their elevational distribution. The two species of *Cypseloides* were found primarily in the subtropical zone; however, little can be inferred from the few records available for the country. *Panyptila cayennensis* and *T. squamata* were also restricted to the tropical lowlands. For species in the genus *Streptoprocne*, specially *S. zonaris*, specific physical or biological factors are more difficult to identify because of their broad elevational ranges, and probably wide daily foraging range.

I found no example of abutting elevational ranges in Ecuadorian swifts that might suggest competitive exclusion. However, in the vertical dimension competitive exclusion seems more likely. When foraging in the same area the species pairs, *P. cayennensis* - *T. squamata* or *S. zonaris* - *S. rutila*, the larger species foraged in the upper strata. Between or among *Chaetura* spp., the species with the larger body size usually occupied the higher stratum. For example, when *C. cinereiventris* foraged with *C. spinicauda*, the former predominated in the upper strata, but when *C. cinereiventris* foraged with *C. egregia*, the latter species seemed to predominate in the upper strata (for body masses see Table 2).

Previous studies on the vertical component in the aerial guild in the lowlands on Central America and Malaysia (e.g., Hespenheide 1975, Waugh 1978, Waugh and Hails 1983) have indicated that flight behaviour, mode of foraging, prey type, and prey size might be important mechanisms of ecological isolation. Further attention to these variables and the behavior of species foraging alone and together may help to clarify possible competitive interactions and resultant resource partitioning mechanisms.

The fourth factor mentioned by Terborgh and Weske (1975), ecotones, does not seem to apply to swifts, because they are so highly mobile that they easily move across such barriers; vegetational distribution patterns probably influence their elevational limits only very indirectly at best.

Many gaps in our knowledge of the distribution and possible resource partitioning still exist for the aerial guild. Although some potential patterns were identified, the few data are available make little more than speculation possible at this point. Further field work on the aerial guild in the tropics, in Ecuador or elsewhere, should look more closely at the vertical component, especially among congeners.

Acknowledgements - I thank Dr. Sergio Figueroa of the Ministerio de Agricultura y Ganaderia and Ing. Miguel Moreno, director of Museo Ecuatoriano de Ciencias Naturales, Quito, for generous assistance in obtaining permits to conduct research in Ecuador. Also, I thank all those that helped through the years of field work in particular: P. Beals, J.M. Carrion, R. Corado, D. Gardner, M. Holmgren, L. Francis Kiff, K. Molina, N.J. Schmitt, and F. Sornoza. I thank the following museums and their curators for specimen information or loans of specimens: Academy of Natural Sciences Philadelphia, British Museum of Natural History, Field Museum of Natural History, Museo Ecuatoriano de Ciencias Naturales, Museo de Zoologia, Universidad del Valle, Cali, Colombia, ex-INCIVA, Museum of Natural Science, Louisiana State University, and Western Foundation of Vertebrate Zoology. Ithank R.T. Chesser, M. Cohn-Head, C.T. Collins, L.F. Kiff, J.V. Remsen and D.A. Wiedenfeld for constructive comments on the paper. Also, I thank N.J. Schmitt who provided the specimen information at the British Museum. The Western Foundation of Vertebrate Zoology and Bleitz Wildlife Foundation supperted the field work in Ecuador; special thanks to their director, Lloyd Kiff, and other personnel.

Resumen - Se examinaron los patrones de distribución elevacional (sobre el nivel del mar) y vertical (sobre el nivel del suelo) a lo ancho de los Andes de las diez especies de vencejos residentes en Ecuador. Tergorgh (1971) y Terborgh and Weske (1975) propusierón cuatro tipos de lìmites que pueden afectar la distribución de los vencejos: 1) "El término natural de un ambiente afectado por una pendiente pudo afectar a sólo dos especies", 2) "Los factores fisicos o biológicos del lugar, que pueden cambiar paralelamente con la inclinación de la pendiente" pudieron afectar a seis de las diez especies; 3) "La exclusión competitiva" no se registro en la pendiente elevacional, pero si parece ser importante en la distribución vertical; 4) No pareció que "los ecotonos" afectaran a la comunidad de aves aéreas.

References

Araya B., Millie G. and Magnere O. 1973. Un vencejo nuevo para Chile: *Chaetura pelagica* (Linnaeus, 1758). *Not. Men. Mus. Nac. Hist. Nat.* No 188: 11-12

Chapman F.M. 1926. The distribution of bird life in Ecuador. *Bull. Amer. Mus. Nat. Hist.* 55:1-784.

Collins C.T. 1968a. Distibutional notes on some Neotropical swifts. *Bull. Brit. Orn. Club.* 88:133-134.

Collins C.T. 1968b. The comparative biology of two species of swifts in Trinidad, West Indies. *Bull. Florida. State. Mus.* 11:257-320.

Eisenmann E. and Lehmann F.C. 1962. A new species of the genus Cypseloides from Colombia. *Amer. Mus. Nov.* 2117.16 pp.

Hartert E. 1892. Catalogue of the birds in the British Museum. 16:434-518. *Taylor and Francis, London.*

Hespenheide H.A. 1975. Selective predation by two swifts and a swallow in Central America. *Ibis* 117:82-99.

Kiff L.F., Marín M., Sibley F.C., Matheus J.C., Schmitt N.J. 1989. Notes on the nest and eggs of some Ecuadorian birds. *Bull. Brit. Orn. Club.* 109:25-31.

Koepcke M. 1964. Las aves del departamento de Lima. *Gráfica Morsom, Lima, Peru.*

Lönnberg E. and Rendhal H. 1922. A contribution to the ornithology of Ecuador. *Arkiv. Zool.* 14:1-87.

Marín M., Carrión B., J.M. and Sibley F.C. 1992. New distributional records for Ecuadorian birds. *Ornitologia Neotropical* 3:27-34.

Marín M. and Stiles F.G. 1992. On the biology of five species of swifts (Apodidae, Cypseloidinae) in Costa Rica. *Proc. West. Found. Vert. Zool.* 4:287-351

Marín M. and Stiles F.G. 1993. Notes in the biology of the Spot-fronted Swift. *Condor* 95:479-483.

Miller H. 1962. Seasonal activity and ecology of the avifauna of an American equatorial cloud forest. *Univ. Calif. Publ. Zool.* 66:1-78.

Paynter R.A. and Traylor M.A. 1977. Ornithological gazetteer of Ecuador. *Museum of Comparative Zoology, Cambridge, Massachusetts.*

Plenge M.A. 1974. Note on some birds in west-central Peru. *Condor* 76:326-330

Remsen J.V. and Cardiff S.W. 1990. Patterns of elevational and latitudinal distribution, including a "niche switch", in some guans (Cracidae) of the Andes. *Condor* 92:970-981.

Remsen J.V. and Graves W.S. Distributional patterns and zoogeography of *Atlapetes* brush-finches (Emberizidae) of the Andes. *Auk* (in press).

Robbins M.B. and Ridgely R.S. 1990. The avifauna of an upper tropical cloud forest in southwestern Ecuador. *Proc. Acad. Nat. Sci. Phil.* 142:59-71

Rogers C.H. 1939. The swifts of Panama. *Auk* 56:81-83.

Salvadori T. and Festa E. 1900. Viaggio del Dr. Enrico Festa nell'Ecuador. Parte terza - Trochili-Tinami. *Boll. Mus. Zool. Anat. Comp. Torino* 15:1-54.

Sick H. 1986. Ornitologia Brasileira, uma introduçãoVol. 1. 2ª. Edição, *Editorial Universidade de Brasília, Brazil.*

Terborgh J. 1971. Distribution on enviromental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcamba, Peru. *Ecology* 52:23-40.

Terborgh J. and J.S. Weske. 1975. The role of competition in the distribution of Andean birds. *Ecology* 56:562-576.

Waugh D.R. 1978. Predation strategies in aerial feeding birds. *Unpubl. Ph. D. thesis*, Univ. of Stirling.

Waugh D.R. and Hails C. J. 1983. Foraging ecology of atropical aerial feeding bird guild. *Ibis* 125:200-217.

Zimmer J.T. 1945. A new swift from central and South America. *Auk* 62:586-592.

Avocetta N° 17: 125-129 (1993)

The diet of the White-rumped Swiftlet (*Aerodramus spodiopygius*) in Queenslands's savannah.

M.K. TARBURTON

P.O. Box 595, Apia, W. Samoa

Abstract Homoptera (planthoppers), Diptera (flies), Hymenoptera (social insects), and Isoptera (termites) were the most numerous prey in 45 food boluses being delivered by parent White-rumped Swiftlets (*Aerodramus spodiopygius chillagoensis*) to their chicks inside six Chillagoe caves. The main food items were planthoppers (47%) and filies (24%), by frequency. The number of insects in each food bolus ranged from 7 to 587 (x = 149). The average weight of a bolus was 0.33 g (range 0.11 - 0.62 g.). The average length of all prey was 3.6 mm, which is larger than the average length of available prey (2.2 mm). The number of prey "species" ranged from 2 to 83 (x = 40) per bolus. A total of 317 invertebrate "species" were recorded in food boluses. The White-rumped Swiftlet breeds during the wet season, when insects are generally accepted as being more abundant. However, the density of potential prey is shown to be significantly lower than that taken during the breeding season in Fiji.

Introduction

The White-rumped swiftlet (*A. spodiopygius assimilis)* takes flies as its most common prey in some seasons in rainforest habitats in Fiji (Tarburton 1986a). Because published studies (Hespenheide 1975, Lack 1956) had not shown flies to be the dominant taxon in the prey of other swifts, it appeared worthwhile to make a comparative diet analysis of this species where it feeds in different habitats and climates. In Fiji this species feeds over rainforest with high rainfall throughout the year. At Chillagoe, Queensland, Australia the same species feeds over savannah habitat where eight months of the year are usually very dry. These are some of the factors which might alter the type and size of the prey taken over the savannah at Chillagoe.

This comparison of the diet of *A. s. chillagoensis* in Australia and A. s. assimilis in Fiji is directed at clarifying the relationship of body size to prey size and whether or not climate and the available food base are determinining factors in diet composition.

Methods

During December 1985, January and December 1986 and January 1987 I studied the food of *A. s. chillagoensis* nesting at Chillagoe, Queensland, Australia (17°S, 144°E). Food boluses were taken from adults caught by a sweep net in narrow sections of caves as they delivered food to their nestings. Boluses were taken from Guano Pot, Gordale Scar Pot, New Southlander, Crack Pot, Keef's Cavern and Golgotha Cave. The approximate locations of these caves are shown in Tarburton (1988), and the methods for collecting and measuring potential prey samples are described in Tarburton (1986a).

During December 1983, January 1984, December 1985 and January 1986, I sampled potential prey of *A. s. assimilis* by attaching a sweep net to a vehicle in similar fashion to Hespenheide (1975).

However, because *A. s. chillagoensis* rarely fed below 8 m I could not sample the air they were feeding in with the net mounted on a vehicle. Instead, I sampled their potential prey by placing the same net as used in Fiji on a five m pole and then I stood on the top of limestone outcrops (Suicide & Spring towers as well as tower number 5126 in Chillagoe township) or on the tank stand at the rear of two Queensland National Parks & Wildlife homes. Swiftlets often fed at these locations and were doing so while some of the samples were being collected. Nine samples were collected in a similar manner in Fiji. Samples were taken by swinging the net through the air in circular and figure of eight motions for five minutes and were spread thoughout daylight hours. This sampling may have been biased by my being able to sample above the tree canopy only where rocky outcrops or other protrusions occured. It could well be that the plant lice were on the plains, which may have been inadeguately sampled.

Accepted 30 December 1993

Statistical reporting is based on mean measurements and their standard errors and is shown in text and tables as x̄ ± se. The data for determining the size of all prey were based on the means of all 45 boluses used in the study rather than that of each taxon so that the extreme means of some of the uncommon types did not swamp those of the majority. Whereas Table 2 shows the actual minimum and maximum sizes of all potential prey netted, those few measurements that were above or below the size that the birds were found to have taken were not used in calculating the average of available prey. It is assumed that insects smaller than the minimum size caught are 'selected against' for perceptual or energetic considerations, and that the one insect that was larger than the maximum caught by the birds sampled, would be too large for the bird to handle.

Results

Identity of prey

Planthoppers were found in all but one of the 45 food boluses and were the most numerous in 18 of them (Table 1) making up 47% (3102 individuals) of the total sample of 6583 invertebrates. Flies were found in 42 of the food boluses, and were the most numerous prey in 11 of them making up 24% of the total sample. Social insects were in 44 boluses and

Table 1. Composition of White-rumped Swiftlet prey in 45 food boluses: Chillagoe, 1985-7

Order	No. of boluses present in	Boluses where dominant	% where dominant	x % ± SE (Range) of occurrence, where present sample	No. in total Sample	% Individuals in total
Homoptera	44	18	36 - 100	37 ± 4.0 (0-100)	3102	47
Diptera	42	11	38 - 56	21 ± 2.7 (0 - 56)	1556	24
Hymenoptera	44	13	42 - 97	27 ± 3.0 (<1 - 97)	1175	18
Isoptera	13	3	48 - 98	28 ± 8.8 (0 - 89)	155	2
Aranae	30	0	0	4 ± 0.6 (0 - 12)	272	4
Heteroptera	23	0	0	4 ± 1.4 (0 - 33)	185	3
Coleoptera	23	0	0	3 ± 0.6 (0 - 9)	112	2
Thysanoptera	10	0	0	<1 (0 - 1)	16	<1
Lepidoptera	6	0	0	2 ± 1.1 (0 - 7)	11	<1
Phasmatodea	1	0	0	<1 (0 - <1)	1	<1
Unidentified	1	0	0	<1 (0 - <1)	1	<1

Table 2. Composition sizes of prey items in boluses of White-rumped Swiftlet and potential prey items in sweep net samples.

	Bolus prey			Potential prey		
Taxon	mean	Range	x %	mean	Range	x %
Homoptera	2.29 ± 0.15	(1.0 - 10.0)	37	1.87 ± 0.14	(1.0 - 2.6)	5
Diptera	2.46 ± 0.13	(1.0 - 9.0)	21	2.05 ± 0.18	(0.8 - 8.5)	39
Hymenoptera	3.62 ± 0.27	(1.0 - 10.0)	27	1.93 ± 0.20	(0.4 - 7.0)	41
Isoptera	6.94 ± 0.60	(3.8 - 10.0)	8	-	(3.2 - 9.0)	2
Araneida	2.38 ± 0.11	(1.0 - 5.5)	3	-	2.0	<1
Coleptera	1.84 ± 0.10	(1.0 - 3.3)	2	2.04 ± 0.02	(1.0 - 6.0)	5
Heteroptera	3.02 ± 0.19	(1.5 - 8.0)	2	-	(1.7 - 2.2)	2
Thysanoptera	1.39 ± 0.17	(1.0 - 2.0)	<1	1.03 ± 0.04	(0.8 - 1.5)	6
Lepidoptera	-	(4.0 - 9.0)	<1	-	9.0	<1
Phasmotodea	-	9.0	<1	-	-	<1
Blattodea	-	-	<1	-	7.0	<1

were the most numerous in thirteen boluses. They made up 18% of the total sample. Termites were the most numerous in three boluses, but beetles, plant bugs (Hemiptera) and spiders were present in more boluses than were termites.

Thirty-one percent (1,669) of the 5,334 insects taken from 24 boluses in the 1985/86 season consisted of just three "species" of jumping plant-lice of the family Psyllidae. The total of 298 species for that season was made up of 90 Hymenoptera, 75 Diptera, 54 Araneida, 36 Homoptera, 25 Coleoptera, 11 Heteroptera, 3 Lepidoptera, 3 Isoptera, and 1 Thysanoptera. The following season in 21 boluses, one species of Phasmodea was found and only 19 new species from the other families were observed in the prey. This took the two year total of prey species to 317.

Size of prey

The largest prey found in this study were three termites and a wasp (a social insect), each 10 mm long. The next largest prey were 9 mm long and included four wasps, a moth, a fly and the only mantid in the sampled prey. Termites were the largest of the common prey, averaging 6.4 mm, then social insects (4.2 mm), plant bugs (3.0 mm), flies (2.5 mm), spiders (2.4 mm) and planthoppers (2.4 mm). The average size of all prey from the 45 boluses was 3.64 ± 0.24 mm (x ± se), which is significantly greater (t_{77} =3.89, p< 0.001), than that of avilable prey (2.4 ± 0.2).

While the average size of prey in each major taxon was not significantly greater than the average size of potential prey (except for the Hymenoptera where t_{78} = 15.2, P< 0.001), the data in Table 2 clearly shows the captured prey to be consistently larger than the available prey. The average size of available prey for the two years was 2.43 ± 0.2 (n = 35) which is significantly smaller than the captured prey (t_{77} = 3.89, P< 0.001). A comparison of the maximum and minimum lengths of potential and actual prey (Table 2) shows that although prey items smaller than 1 mm are available, these swiftlets do not take them. Termites and moths smaller than 3.5 mm are not common in either available or captured prey.

Abundance of potential prey

In the 1985/6 season the sweep-net samples (n = 19) of available prey at Chillagoe caught an average of 9.4 ± 1.6 (n = 19) insects of the size range found to be taken by the birds (1-10 mm). In the following season, which was much drier than the previous season, the average number caught was 5.4 ± 1.4 (n = 21). This was significantly less (t_{38} = 2.1, P< 0.05) than the previous season.

The food bolus

The weight of 32 White-rumped Swiftlet boluses ranged between 0.11 - 0.62 g averaging 0.33 g ± 0.02. The number of insects in a bolus varied from 7 to 587. The average number for all 45 boluses was 146 ± 21. Further analysis of the numbers of individuals and species in the major orders is shown in Table 3.

Table 3. Frequency of major prey in food boluses of White-rumped Swiftlets, Chillagoe (mean ± se)

Order	No of Individuals	No. of Species(a)
Homoptera	71.0 ± 16.0	5.0 ± 1.0
Diptera	35.0 ± 7.0	11.0 ± 1.0
Hymenoptera	26.0 ± 3.0	11.0 ± 1.0
Araneida	6.0 ± 2.0	4.0 ± 1.0
Heteroptera	4.0 ± 2.0	1.0 ± 0.2
Coleoptera	3.0 ± 1.0	2.0 ± 0.4
Isoptera	4.0 ± 1.0	0.4 ± 0.1
Total	149.0 ± 21	32.0 ± 4.0

(a)'Species' is not a named species but is ascribed to individuals that are morphologically similar.

Discussion

Identity of prey compared with that taken in coastal Queensland and Fiji

While flies were numerically the most common invertebrates (43%) in the 32 boluses collected from Fiji swiftlets (Tarburton 1986a) they fell to being the second most common prey (24%) in the 45 boluses collected from swiftlets at Chillagoe. Planthoppers, which made up 24% of the diet and were the second most common prey in Fiji, were the most common prey (47%) in the samples from Chillagoe. Most other taxa were found in similar proportions except for spiders which composed only 1% of prey in Fiji and mad up 4% of prey at Chillagoe; beetles were 7% of prey in Fiji and were only 2% of prey at Chillagoe. Swiftlets feeding over rainforests in coastal Queensland (Smyth 1980), took prey that was more like that of the Fijian swiftlets than those at Chillagoe. Their prey consisted of more flies (50.5%) than plant lice (26.9%) and fewer spiders (2.7%) than were taken by birds at Chillagoe.

The most common flying insects avilable to swiftlets in Fiji and the second most common available at Chillagoe were flies. Whereas in Fiji, the major portion of the prey was flies, they were not the most common prey in Chillagoe. This could be explained if the planthoppers which the Chillagoe birds concentrated on were to be found in swarms or localised areas not sampled with my sweep-net.

Another factor that can cause large variation in the taxonomy of prey in comparative studies, is the variation in prey composition and density that does occur between seasons at the same site (Tarburton 1986a). The estimate of density of available prey found in this study is far below the average of 95 ± 29 (n = 16), insects caught in the same net in Fiji.

If true then the White-rumped Swiftlet in Fiji would appear to have greater ability than most swifts, including *A. s. chillagoensis*, to capture that more manoeuvrable prey (Tarburton 1986b). This is possible as *A. s. assimilis* weighs less and has longer wings than *A. s. chillagoensis*. Since flies are not as large a majority in the available prey at Chillagoe compared to Fiji, this may also help explain their under-representation in the diet of *A. s. chillagoensis*.

Non-fly prey may also be easier to obtain at Chillagoe. Evidence for this is that while Fijian birds forage for 15.5 hours a day, swiftlets at Chillagoe forage for only 13 hours. Fijian swiftlets leave their caves just after 0400 hrs and return for the night mostly after dark between 1930 and 2000 hrs. The majority of swiftlets at Chillagoe do not leave the cave until around 0530 hrs and most return before dark around 1830 hrs.

Swiftlets at Chillagoe are only gathering food for one chick, whereas Fijian swiftlets are collecting food for two chicks. Fijian birds also breed in larger colonies than those at Chillagoe, which means that on overage they have to fly further to their feeding areas. However, we need not appeal to either of these explanations for as was shown in Tarburton (1986a), such variation could result from the time of sampling. Examples given there show that the most abundant taxon in the prey of swifts varies with time, both through a season and between seasons.

A. s. chillagoensis did not take its prey in similar taxonomic proportions to those available within the size range that it handled (Table 2). If it did, social insects would predominate, followed by flies, thrips, planthoppers and beetles. The proportion of each taxon in available prey is very close to that available in Fiji (Tarburton 1986a) as well as in Costa Rica and Panama (Hespenheide 1975), except that thrips equal beetles at Chillagoe and flies were less represented than in Fiji. As Hespenheide (1975) predicted, the proportion of flies caught was below that available. The reason he gave was that the manoeuvrability of flies is said to be better than that of social insects and beetles. However, as Tarburton (1986a) has shown, the proportion of flies in a sample varies largely with the time of sampling and these data may not contradict those from Fiji where flies predominated in only one of the two large samples. Alternatively, one can accept Hespenheide's (1975) suggestion that flies are more manoeuvrable than most insects and that this helps explain their infrequent occurrence in the prey of aerial predators in general. The under-representation of social insects in the diet of swiftlets from both Chillagoe and Fiji does not support Hespenheides' suggestion that the poor manoeuvrability and tendency to swarm make this prey taxon preferred above flies and beetles.

Size of prey

Because *A. s. chillagoensis* (x = 9.3 ± 0.04 g) is significantly larger in body mass (t_{400} = 15.4, P< 0.001) than *A. s. assimilis* (x = 8.19 ± 0.06 g), and because prey size has been positively related to the body size of insectivorous birds (Hespenheide 1971, 1975; Dyrcz 1979), we would expect that *A. s. chillagoensis* would take larger prey than *A. s. assimilis*. The average size of prey taken by *A. s. chillagoensis* (3.64 ± 0.24 mm) was significantly larger (t_{74} = 4.32, P< 0.001) than the average size of prey taken by *A. s. assimilis* (2.48 ± 0.11 mm). However, the available prey sampled by sweep-net was significantly larger (t_{32} = 4.37, P< 0.001) at Chillagoe (2.58 ± 0.17 mm) than at Fiji (1.74 ± 0.09 mm). It has been suggested (Hespenheide 1975) that prey smaller than the minimum size taken is not taken due to either perceptual reasons or because the relative ease of capture for the different taxa converges at small sizes to very similar values.

Conclusions

Although flies were the commonest of the insects available they were second most common to planthoppers in the prey of *A. s. chillagoensis*. However, as only one of the 260 insects caught in the sweep-net was a jumping plant louse, which composed 31% of the prey in the good season, it is clear that the sampling technique was not adequate in all respects. Despite this deficiency it was shown that the swiftlets were taking larger prey than that which was available at some of their feeding sites.

A. s. chillagoensis took larger prey in larger boluses which contained fewer individuals than was the case for *A. s. assimilis*. Each bolus taken by *A. s. chillagoensis* had an average of 10 species more than those taken by *A. s. assimilis*. Thirty-two boluses of invertebrates taken by *A. s. chillagoensis* contained

303 species, whereas the same number of boluses taken by *A. s. assimilis* contained 167 species. That there are no other swifts or swallows resident in the area may help account, as much as the difference in size between Australia and Fiji, for *A. s. chillagoensis* having larger prey of more species available to it than does *A. s. assimilis*.

Aknowledgements - I wish to acknowledge the helpful criticism of the drafts of this paper by Prof Brian Spingett, Charles Collins and E. Bull; and the identification of the plant lice by Dr Ian Stringer of the Zoology Department of Massey University, New Zealand. Chillagoe National Parks staff (J. Barton, D. Flett, J. Fred, L. Leafe and A. Little), were very helpful in allowing entry to their parks and homes for this study. The help of Chillagoe Caving Club memebers (A. Cummins, G. Greaves, Gaylyn Keats, K. Offer, T. Porritt, K. Ridgway and Tom Robinson) in finding and accessing some of the caves was appreciated. I greatefully acknowledge financial help for one of the trips from the Frank M. Chapman Memorial Fund of the American Museum of Natural History. Permission from Queensland National Parks in Brisbane, to carry out this work was appreciated.

Riassunto – Si sono analizzati 45 boli rigurgitati ai pulcini da parte di genitori di *Aerodramus spodiopygius chillagoensis* in sei grotte del Queensland, a Chillagoe. Le prede più numerose sono state: Omotteri, Ditteri, Imenotteri e Isotteri. Il maggior numero di esemplari ritrovati è dato da cicaline (Omotteri) (47%), mosche (Ditteri) (24%). Il numero di prede per bolo varia tra 7 e 587 (media=149). Il peso medio è di 0.33 g (estremi 0.11 - 0.62 g). La lunghezza media delle prede è 3.6 mm, valore superiore alla lunghezza media degli insetti disponibili (2.2 mm). Il numero di specie ritrovate in ciascun bolo varia tra 2 a 83 (media=40). Cumulativamente si sono individuate 317 specie di insetti. *Aerodramus spodiopygius* si riproduce in un periodo considerato secco, quando si pensa che gli insetti siano più abbondanti nell'isola. Nonostante ciò, la densità di prede potenziali in Chillagoe è significativamente inferiore a quella riscontrata nel periodo riproduttivo, nelle isole Fiji.

References

Dyrcz A. 1979. Die nestlingsnahrung bei drosselrohrsanger (*Acrocephalus arundinaceus*) und thichrohrsanger (*Acrocephalus scirpaceus*) and den teichen bei milicz in Polenund zwei seen in der Westschweiz. *Ornithologische Beobachter* 76: 305-316.

Hespenheide H.A. 1971. Food preferences and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. *Ibis* 113: 59-72.

Hespenheide H.A. 1975. Selective predation by two swifts and a swallow in Central America. *Ibis* 117: 82-99.

Lack D. 1956. Swifts in a tower. *Methuen, London.*

Smyth D.M. 1980. Notes on the diet of the Grey Swiftlet (*Aerodramus spodiopygius*). *Sunbird* 11: 20-21.

Tarburton M.K. 1986a. The food of the White-rumped Swiftlet (*Aerodramus spodiopygius*) in Fiji. *Notornis* 33: 1-16.

Tarburton M.K. 1986b. A comparison of the flight behaviour of the White-rumped Swiftlet and the Welcome Swallow. *Bird Behaviour* 6: 72-84.

Tarburton M.K. 1988. Breeding biology of the White-rumped Swiftlet at Chillagoe. *Emu* 88: 202-209.

Avocetta N° 17: 131-138 (1993)

Differences in diet of Common (*Apus apus*) and Pallid (*A. pallidus*) Swifts

MARCO CUCCO[1], DAVID M. BRYANT[2] AND GIORGIO MALACARNE[1]

(1) Dipartimento di Biologia Animale, via Accademia Albertina, 17 - 10123 Torino (I)
(2) Department of Biological and Molecular Sciences, University of Stirling - Stirling FK49 4LA (UK)

Abstract _The diets of Common (*Apus apus*) and Pallid Swift (*A. pallidus*) were compared by faecal and food bolus analysis in a mixed colony in NW Italy. The size of insect-remains increased with age of nestlings in both species. Size (mm) and mean dry mass of insect prey items was greater in the Common Swift. There were also differences in the taxonomic composition of prey: the Common Swift took more aphids in June, and Heteroptera and Coleoptera in July, while the Pallid Swift caught more Acalyptera in June, and Hymenoptera in July . Food balls and faecal analysis agreed in their description of swift diets.
A comparison with aerial arthropod abundance, sampled by suction trap, suggested a positive selection of Hymenoptera and Coleoptera, while Diptera were more frequent in suction trap samples than in the swifts' diets.

Introduction

Aerial feeding birds (e.g. swifts, Apodidae, and swallows, Hirundinidae) are selective in catching their prey, at least during reproduction (Bryant 1973, Hespenheide 1975, Waugh 1979). Larger items than generally available are selected by Swallows *Hirundo rustica*, Sand Martins *Riparia riparia*, House Martins *Delichon urbica* and the Common Swift *Apus apus* (Waugh 1978).

Swifts normally catch insects at higher altitudes than swallows and martins, even when feeding areas overlap, such as during adverse weather (Waugh 1978). Differences in feeding location probably reflect dietary preferences and the flight characteristics as well as the aerial distribution of insects of different types (Waugh 1978).

Of the three generally distributed European species of swifts, the Alpine *A. melba* feeds on moderate-sized arthropods, while the Common and Pallid *A. pallidus* Swifts take both small and moderate size arthropods (Cramp 1985).

Comparison of food preferences amongst species of swifts is difficult because diets can vary geographically. A prevalence of aphids was found in the diet of the Common Swift in Oxford, but this preference varied seasonally. Heterogeneous samples have been detected in the Pyrenees (Glutz and Bauer 1980), Switzerland (Weitnauer 1947) and Italy (Moltoni 1950). Finlayson (1979) in Gibraltar found a large overlap in diet between Common and Pallid Swifts in mixed colonies, even though the latter took a wider range of food including larger prey. A certain degree of niche segregation between the two species is also indicated by structural and behavioural differences: the Pallid Swift has a slighty wider bill and is said to fly lower than the Common, down to 1.5 m (Konig and Konig 1973, Boano 1979, Affre and Affre 1967). This behaviour, however, has only been observed near the colony-sites, where the Pallid Swift usually nests in lower cavities (Cucco and Malacarne 1987), and little is known about the heights of more distant foraging flights.

In this study we analyze by faecal analysis the diets of breeding Common and Pallid Swifts, in order to describe individual differences, seasonal variation, and diet overlap in the two species when there is no geographical segregation.

Methods

The study colony was located in the town of Carmagnola (NW Italy). Both the Pallid and the Common Swifts nested together, in closely spaced (4-5 m apart) cavities situated on the external walls of an old building.

Nestling diets were studied by examining insect remains in faeces produced by the young during their 40-45 days in the nest. In 1991, faeces were collected

Accepted 24 November 1993

at 15-day intervals, from mid-June to August, in 18 nests of the Pallid and 3 of the Common Swift. On each occasion the cavities were completely cleaned out, in order not to mix faeces from different periods. We analyzed 20 samples, obtained from 4 and 3 individual nests of Pallid and Common Swifts during three 15-days periods, to examine for differences between broods. Another four 15-day samples were obtained by mixing the faeces collected in the same period, from 8, 12, 9 and 10 nests respectively of Pallid Swift: these samples represented the full range of the insects taken by the birds at the colony in the four periods. A further sample from a few nests in Spain (Sevilla Cathedral, 24 June 1979) was also considered for the Pallid Swift.

Insect remains in faeces were identified with a binocular microscope, by examination of the wing shape and venation. Identification was made to the order, suborder or family level (Colyer and Hammond 1968, Chinery 1973, 1986) according to the frequency of items and the feasibility of classifying them merely on wing pattern. The size of prey was assessed by measuring intact wing lengths to the nearest millimetre. On average, 149 insects were identified and measured in each sample considered.

Individual insect masses were calculated from wing lengths using the allometric winglength equation: $Y=X^b/D$, where Y=dry weight (mg), X= winglength (mm), b and D are coefficients, different for each taxonomic group of insects, as reported by Turner (1980, 1982).

Another analysis of the taxa eaten by nestlings of Pallid Swifts was obtained in the same colony in 1989-90, using 34 boluses regurgitated by nestlings. In this case the size of prey was not measured.

The availability of insects from different taxa in the area surrounding the colony was estimated by counting the items collected daily from a suction-trap (12.2 m high, captures made during 15/16 days for each half-month period) of the Italian network for aphid control, located in Carmagnola, 3 km North of the study colony.

Results

Sizes of insects and age of nestlings

The size of insects caught throughout the breeding season by Pallid and Common Swifts is shown in Figure 1. In both species we observed an increase in the size of prey correlated with the age of the nestlings, the insects being smaller at the beginning of the rearing period. Differences were statistically significant (Table 1) comparing prey sizes over the first 15-days of age with sizes in the following 15-day period, from either the same nest (A - G) or mixed group of nests. In contrast, at each nest, sizes were similar when comparing the last two 15-day periods (Figure 1, t values ranging from 0.10 to 1.89, P=n.s. for all comparisons).

On the whole, different pairs were similar in the size of selected food items. The size of insects caught in different nests, but in the same period with nestlings of the same age, did not differ between birds of the same species (Figure 1; t tests, P= n.s.). Partial exceptions were found only in two cases for a Pallid Swift nest, which had smaller sizes in the 16-30 June and 16-31 August periods than otherwise, and in one case for a Common Swift nest, where sizes were larger on 1-15 July (t tests, P<0.05). The size of insects in Pallid Swift faeces from Sevilla, Spain, did not differ from those found at the same time of year in NW Italy (Figure 1, t=1.95, P=n.s.).

Insects-sizes in the two species

The distribution of insect sizes in the faeces of Pallid and Common Swifts is shown in Figure 2. The frequency distribution was different in the three 15-

Table 1. Comparison of prey-size in the first and second 15-days periods of rearing.

Nest		First period		Second period	t	N	p
Common Swift	- Nest A	16-30 June	vs.	1-15 July	5.02	272	<0.01
	- Nest B	16-30 June	vs.	1-15 July	2.80	294	<0.01
	- Nest C	1-15 July	vs.	16-31 July	1.64	297	<0.01
Pallid Swift	- Nest D	16-30 June	vs.	1-15 July	4.77	373	<0.01
	- Nest E	16-30 June	vs.	1-15 July	5.75	294	<0.01
	- Mixed	16-30 June	vs.	1-15 July	3.34	277	<0.01
	- Nest F	16-31 July	vs.	1-15 Aug.	2.71	272	<0.01
	- Nest G	16-31 July	vs.	1-15 Aug.	2.58	374	<0.01

Table 2. Comparison of mean prey-size (mm) in the Pallid and Common Swift in 1991 (NW Italy).

Period	**Pallid**			**Common**			**Statistic**	
	Mean	(S.D.	N)	Mean	(S.D.	N)	t	p
16-30 June	3.37	(1.86	713)	3.78	(1.69	388)	3.60	0.01
1-15 July	4.12	(2.07	491)	4.36	(217	363)	1.64	0.10
16-31 July	3.72	(1.85	687)	4.25	(2.04	337)	4.16	0.01

days periods considered (16-30: $\chi^2=59.6$, d.f.=8, $P<0.01$; 1-15 July: $\chi^2=31.7$, d.f.=8, $P<0.01$; 16-31 July: $\chi^2=38.9$, d.f.=8, $P<0.01$). In each period, the prey were smaller in the Pallid Swift (Table 2).

The same result was found when considering the mass of insect prey items (Figure 3): the frequency distribution was different in the three 15-days periods considered (16-30 June: $\chi^2=79.9$, d.f.=7, $P<0.01$; 1-15 July: $\chi^2=20.4$, d.f.=7, $P<0.01$; 16-31 July: $\chi^2=28.0$, d.f.=7, $P<0.01$). Hence, whichever method of size measurement was used, Pallid Swifts were found to take generally smaller prey than Common Swifts.

Differences in taxa

The six principal taxa found in the faeces of Pallid and Common Swifts are shown in Figure 4. A seasonal trend was observed: the Heteroptera were mostly present late in the summer (August) while the reverse was found for the Aphidae. For the other groups seasonal differences were less pronounced. It must also be taken into account that the species of insects contributing to these inclusive categories probably changed during the season.

When comparing the diets of the two species of swifts, the frequency distribution differed significantly between all three 15-days periods (16-30 June: $\chi^2=68.1$, d.f.=5, $P<0.01$; 1-15 July: $\chi^2=33.4$, d.f.=5, $P<0.01$; 16-31 July: $\chi^2=59.6$, d.f.=8, $P<0.01$; 1-15 July: $\chi^2=12.3$, d.f.=5, $P<0.03$). The Common Swift took more aphids in June, and Heteroptera and Coleoptera in July, while the Pallid Swift caught more Acalyptera in June, and Hymenoptera in July.

Comparison of prey in faeces, food-balls and suction trap.

In Table 3 arthropod percentages obtained from the three different sampling methods are reported. Since the data were collected in different years, detailed comparisons are of limited value. Only the greatest differences between aerial insect availability (suction trap data) and prey ingested (faecal and bolus analysis) are therefore examined. The suction trap samples showed a marked prevalence of Diptera in both years. This taxon occurs in the diet, but is not the most abundant food of swifts. On the contrary, swifts eat large quantities of Hymenoptera, which occur at a low frequency in the suction trap samples. Similarly, Coleoptera, captured in relatively small numbers by the trap, were an important component of the swift's diet, especially when determined from faecal samples. Hemiptera (mainly aphids and leafhoppers) show great fluctuations within and between years in our

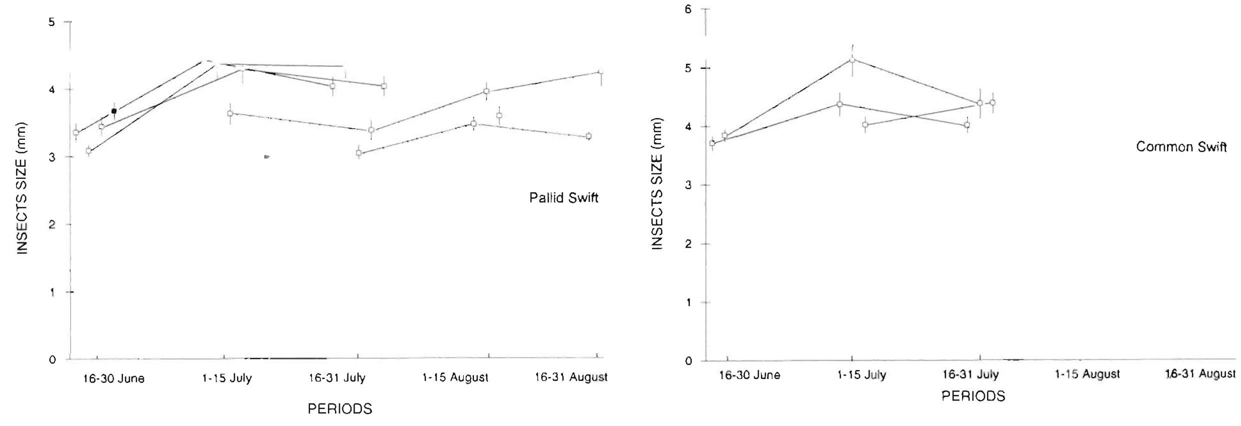


Figure 1. Size of insects (mean ± s.e.) caught in different nests in NW Italy in 1991 (Black square = Sevilla nests, 24 June 1979).

Table 3. Arthropods of different taxa observed in faeces, food-balls and suction trap in NW Italy.

Taxon	16-30 June					1-15 July				16-31July				1-31 July
	FAECES 1991		SUCTION TRAP		FOOD-BALLS	FAECES 1991		SUCTION TRAP		FAECES 1991		SUCTION TRAP		FOOD-BALLS
	Common	Pallid	1989	1990	Pallid	Common	Pallid	1989	1990	Common	Pallid	1989	1990	Pallid
Ephemeroptera	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Odonata	-	0.4	-	-	-	-	-	-	-	-	-	-	-	-
Orthoptera	-	-	-	-	-	-	-	-	-	-	-	-	-	
Hemiptera Het.	4.4	3.2	0.4	0.5	-	12.4	5.9	5.5	1.9	11.6	12.9	2.4	1.0	8.3
Homoptera														
Aphidae	26.5	12.2	25.2	-	6.2	0.3	1.8	6.7	-	1.5	2.1	0.8	0.3	1.6
Cicadellidae	-	-	2.0	1.7	23.9	-	-	1.0	1.7	-	-	1.3	2.7	22.8
Psyllidae	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Other	2.3	1.7	-	-	-	0.3	1.2	-	-	0.3	0.4	-	-	-
Neuroptera	-	-	0.2	0.1	-	-	-	0.3	0.2	-	-	0.6	0.2	-
Coloeptera	33.8	31.7	6.0	4.6	33.0	37.2	39.7	6.9	6.3	29.7	29.5	15.5	6.6	7.6
Trichoptera	-	-	0.1	0.1	-	-	-	0.1	0.1	-	-	0.1	0.1	-
Lepidoptera	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diptera	-	-	65.2	85.7	17.7	-	-	71.2	72.5	-	-	74.7	47.4	30.2
Nematocera	0.3	-	-	3.2	-	0.3	0.2	-	13.1	-	-	-	37.7	-
Tipulidae	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-
Lonchopteridae	-	0.4	-	-	-	-	-	-	-	-	0.1	-	-	-
Phoridae	0.3	0.3	-	-	-	0.6	0.6	-	-	-	-	-	-	-
Syrphidae	1.8	2.2	-	-	-	0.8	3.6	-	-	0.3	2.5	-	-	-
Acalypterates	10.1	22.3	-	-	-	6.9	3.3	-	-	4.5	5.7	-	-	-
Sepsidae	0.3	0.3	-	-	-	-	0.2	-	-	-	-	-	-	-
Sphaeroceridae	1.3	0.7	-	-	-	-	0.2	-	-	-	0.1	-	-	-
Siphonaptera	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hymenoptera	16.8	21.3	0.6	3.1	15.8	38.0	41.5	7.4	3.4	51.6	43.8	2.3	3.2	23.6
parasitic Hym.	2.3	2.9	-	-	-	3.3	1.4	-	-	0.6	2.8	-	-	-
Araneidae	-	0.1	0.2	0.5	3.3	-	-	0.7	0.5	-	-	0.6	0.3	1.4
Other	-	-	0.1	0.5	-	-	-	0.1	0.4	-	-	1.6	0.4	-
N =	388	713	22165	18253	209	363	495	13102	13416	337	682	13336	21934	5695

Table 3. Arthropods of different taxa observed in faeces, food-balls and suction trap in NW Italy.

Taxon	1-15 August			16-31 August			1-31 August	1-30 September		
	FAECES 1991	SUCTION TRAP		FAECES 1991	SUCTION TRAP		FOOD-BALLS	SUCTION TRAP		FOOD-BALLS
	Pallid	1989	1990	Pallid	1989	1990	Pallid	1989	1990	Pallid
Ephemeroptera	0.2	-	-	-		-	-	-	-	-
Odonata	-	-	-	0.2	-	--	-	-	-	-
Orthoptera	-	-	-	-	-	-	-	-	-	-
Hemiptera Het.	34.0	0.8	0.7	62.9	0.6	0.4	-	0.1	0.4	1.0
Homoptera										
Aphidae	3.3	1.3	0.2	-	2.4	0.4	60.8	9.3	16.9	1.5
Cicadellidae	-	0.9	1.1	-	1.4	0.4	-	0. 3	0.6	80.4
Psyllidae	-	-	-	-	-	-	-	-	-	-
Other	2	-	-	1.6	-	-	-	-	-	-
Neuroptera	-	0.4	0.1	-	0.5	0.1	-	0.1	0.1	-
Coloeptera	18.5	10.9	8.2	19.1	9.0	8.2	22.0	2.2	2.9	0.2
Trichoptera	-	0.1	0.1	-	0.8	0.4	-	2.0	1.7	-
Lepidoptera	-	-	-	-	-	-	-	-	-	-
Diptera	-	81.0	39.5	-	79.5	48.4	4.6	70.5	62.6	4.8
Nematocera	-	-	46.0	-	-	34.3		-	17.1	-
Tipulidae	-	-	-	-	-	-	-	-	-	-
Lonchopteridae	-	-	-	-	-	-	-	-	-	-
Phoridae	-	-	-	-	-	-	-	-	-	-
Syrphidae	1.0	-	-	5.2	-	-	-	-	-	-
Acalypterates	4.3	-	-	2.3	-	-	-	-	-	-
Sepsidae	-	-	-	-	-	-	-	-	-	-
Sphaeroceridae	0.8	-	-	-	-	-	-	-	-	-
Siphonaptera	-	-	-	-	-	-	-	-	-	-
Hymenoptera	34.8	2.0	3.4	7.7	3.6	6.0	1.7	4.1	5.2	7.3
parasitic Hym.	2.8	-	-	0.7	-	-	-	-	-	-
Araneidae	-	0.5	0.3	-	0.5	0.6	1.7	1.2	0.6	1.1
Other	-	2.0	0.3	0.2	1.7	0.6	-	1.2	0.8	-
N =	509	11689	16832	439	8705	13633	1151	15959	20736	4437

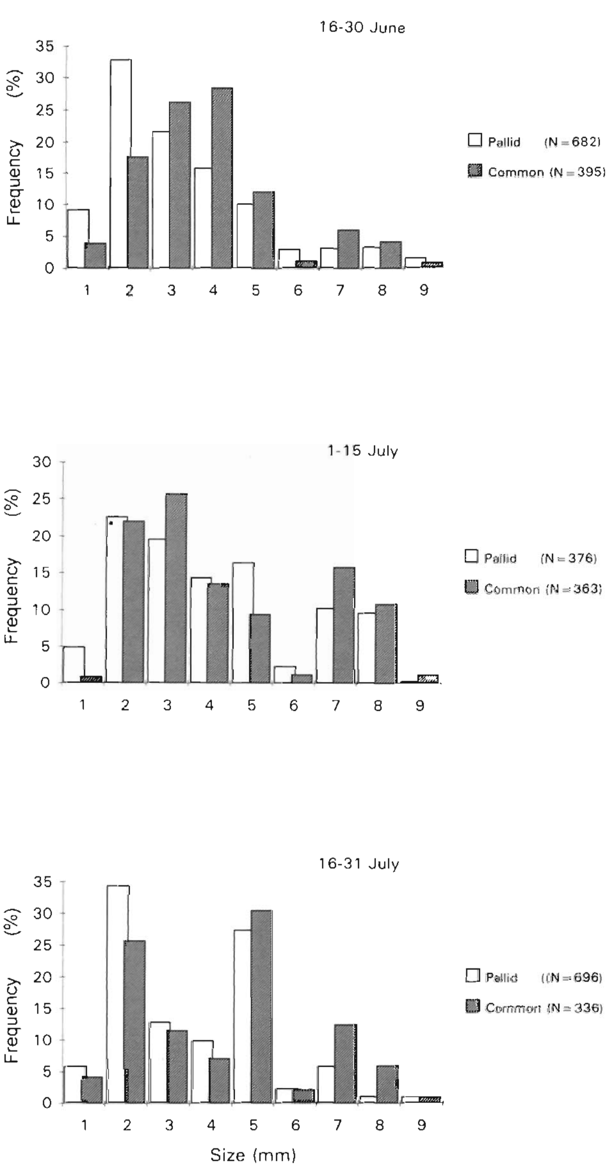


Figure 2. Size of insects caught by Common and Pallid Swifts in different periods in 1991 (NW Italy). Size denotes length of intact wings.

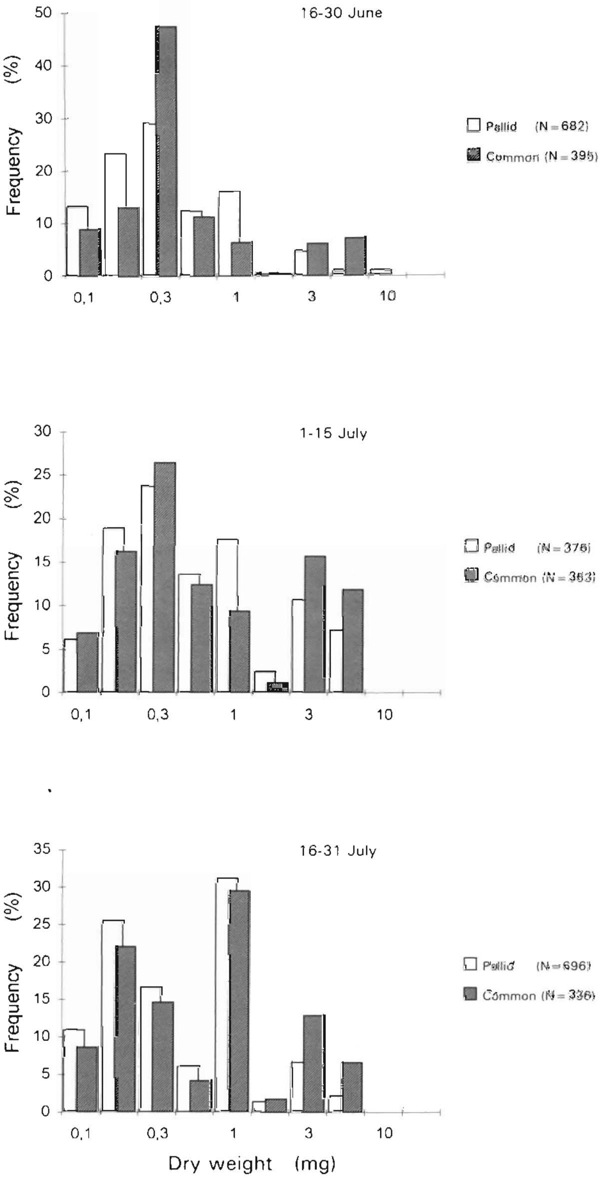


Figure 3. Mass of insects caught by Common and Pallid Swifts in different periods in 1991 (NW Italy).

study-area (Caciagli *et al.* 1989). Accordingly, they seem to appear randomly in the swift diets. On average, however, they seem to be positively selected, since these taxa appear more often in boluses and faeces than in the suction trap.

Discussion

Trophic specialization occurs in many communities of aerial feeding birds (Bryant 1973, Waugh 1978, Hespheneide 1975). Food partitioning is obtained partly as a result of different foraging heights, as shown in the study of a British swallow and swift community (Waugh 1978). However prey diversity is also the product of food selection. In fact when the four aerial feeders (*Hirundo rustica, Delichon urbica, Riparia riparia* and *Apus apus*) living in Britain used the same air space, they reduced competition by increasing the difference in size of the prey they took (Waugh 1978). Moreover, Hespheneide (1975) in a

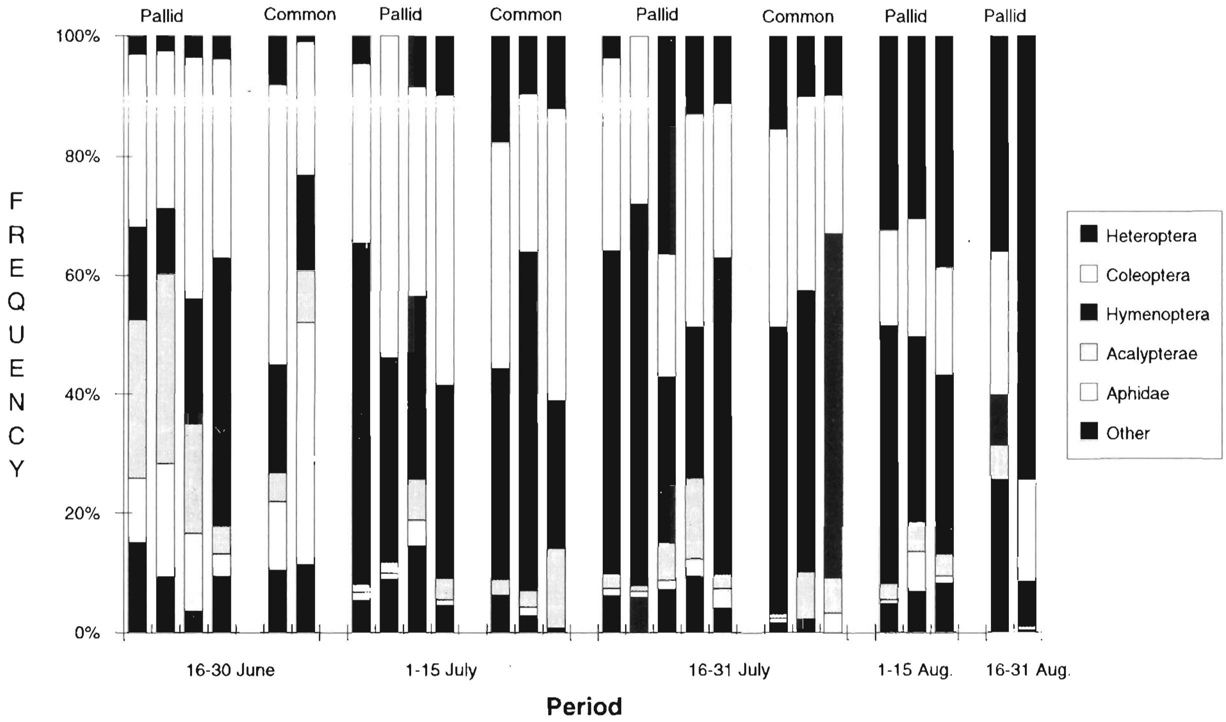


Figure 4. Percentage of insects of different taxa in Common and Pallid Swifts in 1991 (NW Italy). Each column refers to a different nest or group of nests. Common Swifts had left the study area by August.

study of the diets of two swifts and a swallow in a tropical area, found different proportions of taxonomic groups were not explained by preferences alone. He concluded that insect flying agility was important for selection of some prey types and avoidance of others.

The Common and the Pallid Swift show great morphological, ecological and behavioural similarities and breed sympatrically in some Mediterranean areas. Finlayson (1979) showed, on the basis of a small sample from Gibraltar, some diet differences in the two species. The Pallid Swift included big insects (Odonata, Lepidoptera >12 mm) in its prey while the Common Swift never exceeded this size threshold. The Common Swift selected swarms of social hymenopterans and excluded spiders (a common occuring prey type in England, Owen and Le Gros 1954), while the Pallid Swift took both these arthropods as well as many Hemiptera. Our results confirm the existence of diet differences between the two species, but tend to the opposite conclusions about preferred prey sizes. The faecal analysis has shown that insects eaten by the Common Swift are significantly larger in size. On the whole, in our analysis, the Pallid Swifts ate more Dipterans and Hymenopterans, while the Common Swift ate more Aphids and Coleopterans.

Some further points have to be considered.

1) Faecal analysis may give different results from those obtained from food-bolus analysis. Different digestibilities of prey may result in under or overestimation of some taxa. For example, particularly large items are often broken down in faeces while smaller more flexible ones survive, so there may be a bias against relatively large items in faecal samples, which would nevertheless appear in food balls. Faecal analysis represents the average diet taken over a certain period. On the other hand, food-ball studies usually utilize items collected over a few hours or days. The previous studies on the Pallid Swift diet (Finalyson 1979, Bigot *et al.* 1984 for example) were probably too restricted in this respect. Finalyson (1979) concluded that dietary differences between the two species exists, on the basis of a sample in June, while more prolonged monitoring could have led to other conclusions, since the overlap between the species is obviously considerable.

2) It is quiet clear that aerial feeders often depend on unpredictable spatio-temporal accumulations of aerial arthropods. Swarming of ants, bees, aphids, termites and ladybird beetles can lead to massive local accumulations of prey and the opportunistic

exploitation of these constantly changing resources induces a very high intraspecific variability in diets (Lack and Owen 1955). This pattern is evident in data from the same nest in different time periods, or even between two close nests on the same day (Malacarne and Cucco 1992).

3) Aerial insectivores forage selectively. In the House Martin, the closest correlation with available food supply was found in the nestlings diet when there was a high relative abundance of large insects, but food selectivity was not associated with changes in the aerial insect diversity (Bryant 1973). It is more difficult, on the basis of the same method, to assess food selectivity in swifts. The proportion of insects eaten by swifts is in general very different from that observed with the suction trap (12.2 m high). This is likely to be due to a difference in the altitude at which swifts and martins forage. It is therefore unlikely that the suction trap catch accurately reflected the insects encountered during foraging, at a great height and over a very wide area.

4) In spite of an obvious diversity in diet composition, there was some constancy in the type of arthropods eaten by swifts. The prey taxa invariably included Hymenoptera, Diptera, Hemiptera (both Homoptera and Heteroptera) and to a lesser extent Coleoptera. Some inconsistencies could be due to a limited sample size. For the Pallid Swift, for example, the unusual importance of Araneae reported in Morocco (Bigot *et al.* 1984) could be due to a very short time over which samples were collected.

The generality of the importance of certain taxa to aerial feeding birds is illustrated by the fact that tropical swiftlets (*Collocalia esculenta, Aerodramus spodiopygius*) mainly eat the same four insect taxa cited above (Hails and Amirudin 1981, Tarburton 1986).

Acknowledgements - The research was supported by 40-60% M.P.I. founds to G. Malacarne.

Riassunto - L'analisi dei resti fecali e dei boli rigurgitati ai pulli ci ha permesso di effettuare un'indagine in contemporanea sull'alimentazione di Rondoni comuni e Rondoni pallidi nidificanti nella stessa colonia. Esiste una buona corrispondenza tra le due metodiche nel descrivere la scelta giornaliera delle prede. Le dimensioni dei residui entomologici aumentano con l'età dei pulli in entrambe le specie. Le dimensione dell'ala e il peso secco delle prede sono risultate maggiori nel Rondone comune. Esistono inoltre differenze nella composizione della dieta: il R. comune cattura più afidi in giugno, eterotteri e coleotteri in luglio mentre il R. pallido ha catturato più ditteri acalipteri in giugno e imenotteri in luglio. Una comparazione giornaliera con gli artropodi aerei disponibili, campionati mediante torre a suzione, suggerisce che i rondoni selezionino positivamente imenotteri e coleotteri, mentre i ditteri sono percentualmente più frequenti nel campione aereo che non nei resti fecali o nei boli.

References

Affre G. and Affre L. 1967. Observations automnales sur une colonie de Martinets Pales, *Apus pallidus*, à Toulouse. *Alauda* 35:108-117.

Bigot L., Ponel Ph and Thevenot M. 1984. Note sur le regime alimentaire des jeunes Martinets pales *Apus pallidus* (Shelley) au Maroc. *Bull. Inst Scient Rabat* 8:149-156.

Boano G. 1979. Il rondone pallido *Apus pallidus* in Piemonte. *Riv. ital. Orn.* 49:1-23.

Bryant D.M. 1973. The factors influencing the selection of food by the house martin (*Delichon urbica* (L.)). *J. Anim. Ecol.* 42:539-564.

Caciagli P., Casetta A. and Conti M. 1989. Aphid vectors of plant viruses migrating in North-West Italy. In: (Cavalloro R., ed.) *"Euraphid" Network: trapping and aphid prognosis.* Commission of the European Communities, p. 221-235.

Chinery M. 1973. Insects of Britain and Northern Europe. Collins, London, 352 pp.

Chinery M. 1986. Insects of Britain and Western Europe. *Collins, London* 320 pp.

Colyer C.N. and Hammond C.O. 1968. Flies of the British Isles. *F. Warne & Co. Ltd, London*, 384 pp.

Cramp S. 1975. Handbook of the birds of Europe, the Middle East and North Africa. *Vol. 4. Oxford Univ. Press, Oxford.*

Cucco M. and Malacarne G. 1987. Distribution and nest -hole selection in the breeding pallid swift. *Avocetta* 11:57-61.

Finlayson J.F. 1979. The ecology and behaviour of closely related species in Gibraltar with special reference to swifts and warblers. *Unpublished D.Phil. Thesis, Oxford University.*

Glutz Von Blotzheim U.N. and Bauer K.M. 1980. Handbuch der Vogel Mitteleuropas 9. *Aula Verlag, Wiesbaden*

Hails C.J. and Amirudin A. 1981. Food samples and selectivity of White-bellied swiftlets *Collocalia esculenta. Ibis* 123:328-333.

Hespeneide H.A. 1975. Selective predation by two swifts and a swallow in Central America. *Ibis* 117:82-99.

Konig I. and Konig C. 1973. Nueva contribution para el concocimiento de la avifauna de la costa brava septentrional. *Ardeola* 19:49-55.

Lack D. and Owen D.F. 1955. The food of the swift. *J. Anim.* Ecol. 24:120-136.

Malacarne G. and Cucco M. 1992. Preferenze alimentari del Rondone pallido, *Apus pallidus*, in Piemonte. *Riv. Piem. St. Nat.* 13:89-96.

Moltoni E. 1950. Dati positivi sull'alimentazione dei rondoni (*Micropus*) in Italia. *Riv. ital. Ornit.* 20:140-144.

Owen D.F. and Le Gros A.E. 1954. Spiders caught by Swifts. *Ent. Gaz.* 5:117-120.

Tarburton M.K. 1986. The food of the white-rumped Swiftlet (*Aerodramus spodiopygius*) in Fiji. *Notornis* 33:1-6.

Turner A.K. 1980. The use of time and energy by aerial feeding birds. *Unpubl. PhD. Thesis, University of Stirling,* UK.

Turner A.K. 1982. Optimal foraging by the swallow (*Hirundo rustica*, L.): prey size selection. *Anim Behav.* 30:862-872.

Waugh D.R. 1978. Predation strategies in aerial feeding birds *Ph.D. Thesis, University of Stirling.*

Waugh D.R. 1979. The diet of Sand Martins Riparia riparia during the breeding season. *Bird Study* 26:123-128.

Weitnauer E. 1947. Am Neste des Mauerseglers, *Apus apus. Orn Beob.* 44:133-182.

Avocetta N° 17: 139-140 (1993)

Black Swift (*Cypseloides niger*) nesting site characteristics: some new insights

OWEN A. KNORR

Institute for Alpine Ecology, 4535 Lakewood Court - Reno, Nevada 89509 USA

Abstract – Thirty years ago, a study of Black Swift nesting sites resulted in the establishment of a set of five nesting site characteristics for this species subsequently confirmed by other researchers. New findings suggest the modification of one of these and the addition of a new one. These findings are discussed.

Introduction

A 10-year study I conducted was to determine the geographical distribution of the Black Swift (Cypseloides niger) in the state of Colorado USA and the physical ecological factors influencing this distribution (Knorr 1961). This resulted in the discovery of 27 active breeding colonies consisting of 80 nests and a set of five nesting site characteristics common to all of them: water, high relief, inaccessibility, darkness, and unobstructed flyways immediately in front of the nests. Subsequent work by other researchers confirmed the presence of these characteristics with minor variations (Hunter and Baldwin 1962, Foerster and Collins 1990) and they have been present at other breeding sites discovered since then in the states of Utah and Arizona (Knorr 1962,1989). More recently, my analysis of a large Black Swift site in the state of California and two potential sites in the state of Idaho suggests the modification of one characteristic and the addition of a new one. The purpose of this paper is to set forth these findings and the reasons for the changes in the previously established nesting site characteristics. For clarity, the paper has been divided into two parts.

Part I - Methods

Of the almost 40 Black Swift nesting sites I have studied, nearly all have exhibited 'high relief'. That is to say, they have been situated in a commanding position above the surrounding terrain so that birds flying out from the nests on a horizontal course find themselves automatically at feeding altitude above the adjacent valley. However, the nesting site of a large group of Black Swifts (8-10 pairs) located at Burney Falls in McArthur Burney Falls State Park, Shasta County California has been studied recently and seems to differ to a certain extent from a strict application of the factor of high relief. The waterfall is at an elevation of 900 meters on Burney Creek and drops 40 meters into a gorge which leads to Lake Britton 1/2 kilometer away, a dammed portion of the Pit River. The surrounding terrain is flat table land into which Burney Creek has cut the waterfall and subsequent stream gorge. Consequently when one stands at the edge of the gorge, the falls appear to be in a depression rather than occupy-ing a position above the surrounding terrain except in the direction of stream flow. Several days of di-rect observation of this site on different occasions during the breeding seasons of 1988-1992 were conducted to understand the implications of this lack of the usual high relief found at Black Swift nesting sites.

Results

It is possible for the swifts to fly straight out horizontally from the nests and down the gorge to Lake Britton where most of the birds feed. However, this requires flying a winding course between the trees lining the gorge before achieving open air space over the lake, and only an estimated 10% of departing birds use this route. The remaining birds have adapted to the lack of a complete high relief nesting situation with a behaviour not seen before at any other Black Swift nesting site. They perform an orbiting climb in the air space in front of the waterfalls, which is a rough cylinder 60 meters in diameter, averaging an

---

Accepted 30 December 1993

estimated three complete circles before reaching sufficient altitude to clear the surrounding terrain and trees and to depart the area on feeding forays.

Discussion

Although all the other Black Swift nesting site characteristics are present at the Burney Falls site, the factor of high relief is only partially present. To accomodate this unique situation, we believe that the factor of high relief as a Black Swift nesting characteristic should be described as being 'almost invariably' present.

Part II - Methods

In searching for Black Swift nesting sites in the state of Idaho in 1990, two waterfalls carrying a heavy flow of water were found on the Henry Fork of the Falls River. Named Lower and Upper Mesa Falls, they are in extreme eastern Idaho near West Yellowstone and the border of Wyoming, and are 20 and 35 meters high respectively. All five Black Swift nesting site characteristics are present at both waterfalls and from past experience appeared very likely to be suitable Black Swift nesting sites.

Results

Although it was the height of the Black Swift nesting season, no birds appeared and none was observed in the vicinity. The conclusion was that Black Swifts were not nesting at these sites which were then studied in detail for reasons for the absence of the birds.

Discussion

Until recently, studies of the nesting of the Black Swift have been directed to where they nest (geographic distribution) and why they nest where they do (physical ecological factors). No attention had been paid to why they were not present at sites which otherwise provided the customary nesting site characteristics. At the Idaho sites, the native rock over which the waterfalls flowed and which surrounded the falls was basalt and andesite, a particularly hard and smooth rock whose surface provided no pockets, crannies, ledges, or shelves in the rock for the placement of nests. Foerster and Collins (op cit) in their study of the breeding distribution of the Black Swift in southern California included a list of 36 waterfalls where no Black Swifts nested although some of the sites appeared to provide the five classical nesting factors. Their conclusion that "...some clearly lacked a suitable ledge or shelf to support a nest..." agrees with what was found at the Idaho sites. I believe that this factor accounts for the absence of Black Swifts at the Idaho sites as well as at other likely waterfalls which support no breeding swift population. Accordingly, we believe that a sixth nesting site characteristic should be added to the five previously established: 'Presence of niches in rock for nests'.

Riassunto - Uno studio svolto trent'anni fa sui siti di nidificazione di *Cypseloides niger* aveva indicato 5 caratteristiche tipiche per l'insediamento di questa specie. Recenti ricerce suggeriscono la modificazione di una di esse e l'aggiunta di una inedita caratteristica.

References

Foerster K. and Collins C. 1990. Breeding Distribution of the Black Swift in Southern California. *Western Birds* 21:1-9.
Hunter W. and Baldwin P. 1962. Nesting of the Black Swift in Montana. *Wilson Bull.*74:409-416.Knorr 0. 1961.
Knorr 0. A. 1961.The geographical and ecological distribution of the Black Swiftin Colorado. *Wilson Bull.*73:155-170.
Knorr 0. A. 1962.Black Swift breeds in Utah. *Condor* 64:79.
Knorr 0. A. 1989. The Black Swift in the Chiricahua Mountains of Arizona. *Southwest.Naturalist* 34:559-560.

Avocetta N° 17: 141-146 (1993)

Call types of the Common Swift *Apus apus*: adult call given at the nest

VINCENT BRETAGNOLLE

CEBC-CNRS, F-79360-Beauvoir sur Niort, France

Abstract - Vocalizations of the Common Swifts were studied during two consecutive springs in southern France. I found that three call types were given by the adults at the nest, and these are described quantitatively. Significant differences in the acoustic parameters of the calls are highlighted, as well as a probable sexual dimorphism. This, together with the precise signification of the different call types, remain however to be critically assessed by playback experiments.

Introduction

Swifts (Order Apodiformes) are unusual among birds because many of their life history traits (i.e. longevity, delayed maturity, large egg size) make them atypical compared to similar-sized birds (Lack 1956, Gaillard *et al.* 1989), and convergent evolution of life histories with, e.g., long lived seabirds such as Procellariiformes, have been suggested repeatedly (e.g. Lack and Lack 1951, Malacarne *et al.* 1991). Although investigations have been carried out on the Common Swift *Apus apus* with regard to demography (Lack 1956, Perrins 1971, Lebreton *et al.* 1992), diet (Owen 1955), metabolism (Koskimies 1950), and breeding biology (Lack and Lack 1951, Lack 1956, Gory 1987), nearly nothing has been published on its vocal behaviour (Cucco *et al.* 1987). The only studies available are incomplete sketches of the calls of either the common swift or the Pallid Swift *A. pallidus* (Cramp 1985, Cucco *et al.* 1987, Malacarne *et al.* 1989, Malacarne and Cucco 1990. Cucco *et al.* in press), or concern their peculiar "social flights" (Farina 1980,1988). In this paper I report some preliminary results on the calls of the Common Swift, derived from a more complete study that focuses on the behavioural ecology of three swift species (*A. apus, A. pallidus* and *A. melba*), in which mating, mate retention and coloniality are the main topics covered.

Methods

Common Swifts were studied during April, May and June 1991 and 1992 in the city of Nîmes (southern France), where a large colony is easily accessible for field studies (for further details, see Gory, this volume). A sample of 22 accessible nests was selected, for which extensive data on breeding biology and breeding success were also available dating from 1978 (Gory et Jeantet 1986). The birds were tape recorded by Uher 4400 or Nagra IV at a speed of 19.5 cm/s, on Agfa PE43 tapes, and with a Seinnheiser omnidirectional microphone MD421 placed within, or at the entrance of, the nesting cavity. Calls were analysed on a Real Time Spectrograph, which performs a fast Fourier transform (Richard 1991) at a 7000 Hz bandwith and 256 points stepsize. A total of 252 calls from 13 nests were analysed. The physical parameters studied were (Figure 1): total duration of syllable (SYL), number of syllables per call (NSY), modal frequency (MOF) of the syllable (defined as the frequency carrying the maximum energy when averaged over the whole call and the fundamental frequency at its highest value (FUN). In the case of the Duet Screaming Call, which is given sometimes in long series of antiphonal songs (Malacarne and Cucco 1990). only the first two or three syllables were analysed (syllable ranks 1 to 3). Temporal, and frequency parameters, were measured to within ± 3ms and ± 26 Hertz respectively. Sonagrams were printed on a Kay 6061B Sonagraph (wide and narrow bands). In the following, I will use Cramp (1985) as a starting reference work.

Statistical analysis was performed mainly with the Analysis of variance (ANOVA) when distributions of the call parameters did not depart from normality, and Kruskall- Wallis and Mann-Whitney U-tests for discrete variables (NSY). My aims were to investigate

Accepted 30 December, 1993

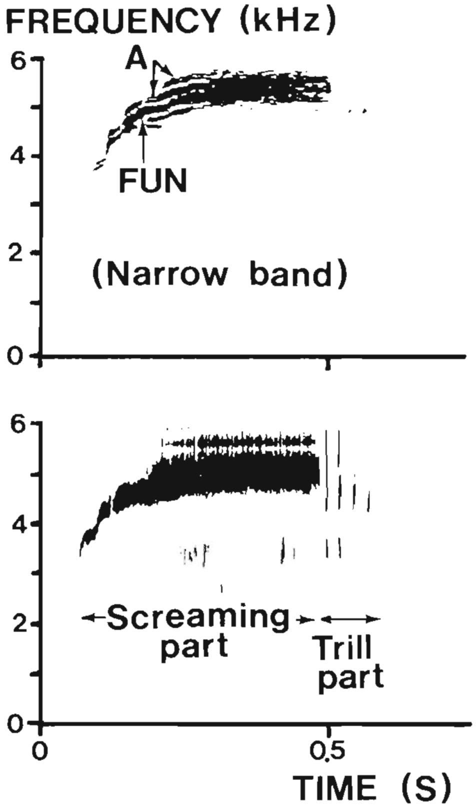


Figure 1. Sonagram of a Common Swift *Apus apus* screaming call (Long Screaming Call) showing some acoustic parameters that were analysed. The difference between the Screaming part and the trill part is shown. The total duration of the syllable (SYL) included the Screarning and the Trill parts. The arrow (A) denotes the occurrence of the amplitude modulation at ca. 200 Hz on the fundamental frequency.

for possible significant effects of the following factors on the call parameters that were analysed: call type, syllable rank (only in duet calls), and nest number (i.e. individual). To this end, I used two-way ANOVAs, with nest and call type as the two factors, and one-way ANOVA when considering syllable rank.

Results

Vocal repertoire of the Common Swift

The most commonly uttered call of the Common Swift, whether at the nest or when flying, is the screaming call (Cramp 1985). However, I found that the screaming call consisted more of a family of highly variable calls, rather than being a call itself, and it was found actually to encompass two different vocalizations. Screaming calls at the nest were given in a highly variable number of syllables, as swifts uttered either a single syllable, or gave the screaming calls in duets (antiphonal song: Malacarne and Cucco 1990). However, monosyllabic screaming calls could be given in a short duration version, similar to the first syllable of a duet call, or in a much longer version (Table 1). This latter vocalization should thus be described as a new call, hereafter referenced as the Long Screaming Call (LSC). Conversely, the other version, whether given in duet or not, will be named the Duet Screaming Call (DSC). Furthermore, a third call type was frequently heard, already described as the "nest call" (in Cramp 1985). In the following, I shall describe the physical structure of the screaming calls, as it is somewhat complex.

Acoustic features of the screaming calls

Although screaming calls are highly variable (see below), I found however that some acoustic features were stable; for instance, the screaming call could always be split into a screaming part sensu stricto, and a trill part ("terminal part" of Malacarne and Cucco 1990; see Fig. 1). The physical structure of the screaming part of the call results from a combination of two acoustic phenomena: first, the fundamental frequency lies around 2500 Hz, and always displays at least its first harmonic (often, only the harmonic can be detected on the sonagram), which thus lies around 5000-6000 Hz (for this study; see also Malacarne et al. 1989). Second, on the fundamental frequency, there is an amplitude modulation at ca. 200 Hz (range 190-280 Hz in this sample), which is the origin of the "clicking" or pulsating sound of Common Swift calls (Figure 2). The trill part is made of a variable (both between-, and within-individuals) number of very short syllables (three to eleven in this sample). The fundamental frequency decreases in the trill part (see also Malacarne *et al.* 1989), and there is no amplitude modulation in the trill part. Interestingly, the trill part is very distinct between the two members of a pair: invariably, one partner has a fast rhythm trill (with very short duration elements and silences between elements, and a greater number of elements), and the other one has a slower rhythm (Figure 2 see also Cucco *et al.* in press). The differences in durations, as well as in the number of elements in the trill, are highly significant (Table 2). This was already illustrated in sonagrams of Cramp (1985) and Malacarne and Cucco (1990), though these authors did not elaborate on this point. Of course, this is likely to represent a sexual dimorphism in the trill part, although the sample size of sexed birds is too small at present to establish this definitely. According to the

Table 1. Call types of the common swift *Apus apus* given at the nest. For the Duet Screaming Call, the first three syllables were analysed separately (ranks 1 to 3). See Figure 1 for the physical parame were analysed. A one way ANOVA was conducted to test for the effects of call type on each parameter; a two-way ANOVA was also conducted in order to compare the effects of nest (i.e. individual) and call type (DSC type A and DSC type B) on the call parameters.

Call type	Call parameters				
	Sample size[1]	Syllable length[2] (SYL) (MOF)	Modal frequency[3] (FUN)	Fundamental frequency[3] (NSY)	Number of syllabes
Long Screaming call (LSC)	22(6)	654.3±108.8	3966.2±1738.	16103.3±328.	61.0±0.0
Duet Screaming Call A (DSC)	100 (10)	04.0±86.1	5034.6±979.9	5494.4±461.4	3.01±1.8
Rank 1	53	449.3±86.5	5062.3±994.3	5484.6±502.9	/
Rank 2	41	352.4±51.9	5018.8±968.4	5495.6±420.3	/
Rank 3	6	355.7±33.6	4896.8±1094.4	5572.3±403.4	/
Duet Screaming Call B	99 (10)	397.5±65.0	5282.3±536.4	4866.1±928.4	2.85±2.1
Rank 1	63	419.4 ± 68.4	4899.7 ± 854.6	5201.7 ± 525.5	/
Rank 2	32	359.3±35.2	4842.0±1051.1	5420.2±547.3	/
Rank 3	4	358.0±25.3	4525.3±1209.4	5447.8±472.8	/
Nest Call	31(5)	101.3±22.4	4151.0±230.1	/	/
One-way ANOVA	df		(F-value)		
Call type	2	36.9***	2.03	13.99***	19.22****[4]
Rank effect	2	34.95***	0.27	2.30	
Two-way ANOVA					
Nest effect	9	6.23***	8.80***	3.81***	50.45****[4]
Call type effect	1	7.32**	15.2***	16.13***	1.35 [5]
Nest X Call type	9	1.46	1.35	1.88*	/

[1]: Number of calls analysed, and number of individuals sampled between brackets; [2]: measured in ms; [3]: measured in hertz;
[4]: Kruskall-Wallis test; [5]: Mann-Whitney U-test
*,p<0.05; **, p<0.01; ***, p<0.001.

Table 2. Temporal parameters of the trill part of the Duet Screaming Call. Type A and Type B compared (see text). Only five pairs were analysed here, due to insufficient sample size.

Call type	Sample size [1]	Short syllable duration	Inter-syllabic duration	Number of short syllables
Duet Screaming Call				
Type A	18	10.31±2.5	5.61±5.1	8.56±2.2
Type B	16	14.2±3.0	11.43±4.6	6.31±1.5
t-test		7.6***	6.6***	3.31*
df		120	120	32

[1]: refer to the number of Duet Screaming Calls that were analysed.

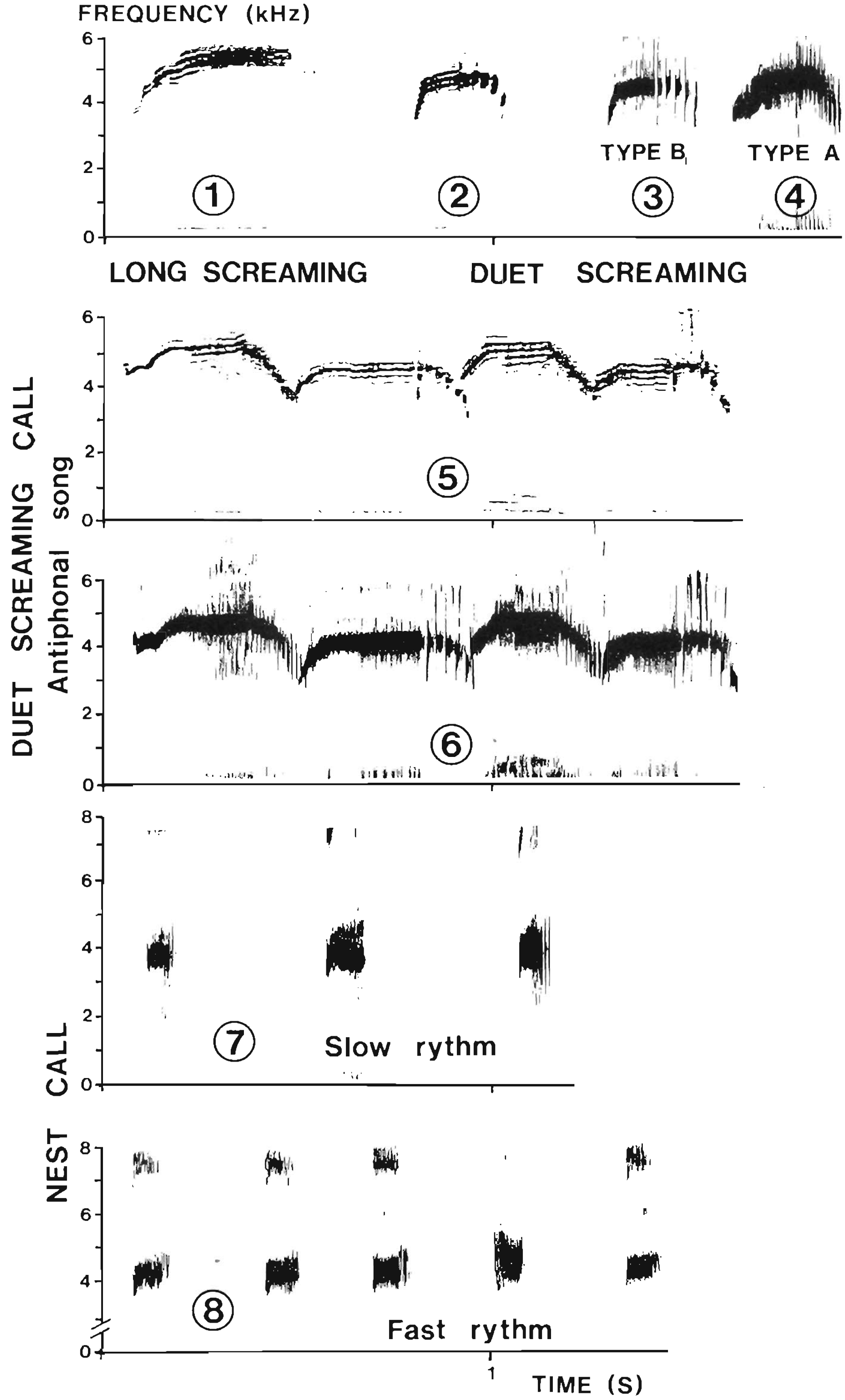


Figure 2. Sonagrams of the three call types that are uttered by the Common Swift *Apus apus* at the nest: the Long Screaming Call (1; see also Fig. 1), the Duet Screaming Call (2, 3, 4, 5 and 6) and the Nest Call (7 and 8).
Note the difference in the trill part (Type A and B) on the duet screaming call (3 and 4). Note also that the rhythm of the nest call is variable (7 and 8). Time is given in seconds and frequency in KiloHertz. Sonagrams were printed using wide band filter (300Hz) except for 1, 2, and 5 (narrow band, 45 Hz).

results found for the Pallid Swift, males probably have the fastest trill part (Cucco *et al.* in press). Until we get more sexed birds, type A (fast rhythm in the trill part) and type B (slow rhythm) screaming calls will be retained.

Long and Duet Screaming Calls share many similarities, and some overlap may occur between individuals but not within individuals: LSC are always much longer than DSC for any given individual (see also F-values on Table 1). Thus the LSC is statistically longer than the DSC, being usually twice as long as the DSC (Table l) and often, but not necessarily, higher in frequency.

Discussion

The Long Screaming Call, during this study, appeared to be given only by the presumed males, but the sample size is far too small at present to exclude the possibility that females utter this type of call. It was also found to be given mainly at the start of the breeding season, and most often in response to an intruder visit in the nest cavity. It is therefore tentatively suggested that the LSC is mainly a territorial and/or an agonistic call.

The Duet Screaming Call, which is usually given in duets, probably also has a territorial function, as it is often uttered after the LSC, following the intrusion of a third bird into the nesting cavity, but I suggest that it has other functions. First, the DSC is individually distinctive (see Table 1 for F-values with regard to nest effect) and may thus function as a cue in individual/partner identification (see, *e.g.* Bretagnolle 1989, Bretagnolle and Lequette 1990 for similar studies). Malacarne and Cucco (1990) suggested that the "terminal part" (or trill) is very constant within individuals, though I found that the number of syllables were partially variable. Second, the DSC may also function as a synchronising behaviour (see also Malacarne and Cucco 1990).

Lastly, the Nest Call (NC; Cramp 1985; see Table l) is often given by birds within their nests. However, unlike Cramp (1985), I found that it was given by a single bird (as stated in Cramp 1985) but always in a situation where the pair is present. Moreover, I found that it was the presumed male which gave it, and not the female (as stated by Cramp 1985), but this has to be checked further. This call was only given by the pairs without eggs (i.e. before egg-laying for the breeders, or at any time for the non breeders). I thus suggest that the NC has a sexual function, being involved in mating or re-pairing for established pairs.

The speculative nature of many of these results has now to be critically tested experimentally using playback tests on birds with known age, status and sex.

Acknowledgements - This work is part of a collaborating project with G. Gory, and I thank him very much for sharing his knowledge of swifts, providing advice on numerous occasions and reading a previous draft of this paper. I thank also R. Jeantet (Conservateur au Museum de Nîmes) and the staff of the Museum for giving me the opportunity to work there in exceptionally good conditions. Lastly, I acknowledge with gratitude J. F. Ward who improved the english, L. Ruchon who drew the Figure, and Dr. G. Malacarne and an anonymous referee for constructive criticism on a previous draft.

Riassunto - Si descrivono quantitativamente le vocalizzazioni del Rondone comune nel Sud della Francia. Si sottolineano le differenze dei tre tipi principali di grida emesse dal nido ed alcuni aspetti sessualmente dimorfici. Il significato delle vocalizzazioni potrà essere stabilito solo con opportuni esperimenti di playback.

References

Bretagnolle V. 1989. Calls of Wilson's storm petrel: functions, individual and sexual recognition, and geographic variation. *Behaviour* 111: 98-112.

Bretagnolle V. and Lequette B. 1990. Structural variation in the call of the Cory's shearwater (*Calonectris diomedea*, Aves, Procellaridae). *Ethology* 85: 313-323.

Cramp S. (Ed.). 1985. Handbook of the Birds of Europe, the Middle East and North Africa. Vol. IV, Terns to Woodpeckers. *Oxford Univ. Press, Oxford.*

Cucco M., Malacarne G., Griffa M., Piazza R. and Boano G. 1987. A comparative approach to the behavioural ecology of swifts. *Monitore Zool. Ital.* 21: 182-183.

Cucco M., Malacarne G. and Poncino, A. In press. Duet vocalizations in the Pallid Swift *Apus pallidus:* context in which they occur and sexual dimophism. Atti 6° Convegno Italiano di Ornithologia. *Boll. Mus. Sc. Nat. di Torino.*

Farina A. 1980. Some observations on the social behaviour of the swift *Apus apus* (L.) during the breeding season. *Monitore Zool. Ital.* 14: 106.

Farina A. 1988. Observations on the swift *Apus apus* (L.) social flights at the breeding sites. *Monitore Zool. Ital.* 22: 255-261.

Gaillard J.-M., Pontier D., Allaine D., Lebreton J. D., Trouvilliez J. and Clobert J. 1989. An analysis of demographic tactics in birds and mammals. *Oikos* 56: 59-76.

Gory G. 1987. Influence du climat mediterraneen sur la reproduction du Martinet noir (*Apus apus* L.). *L'Oiseau et la R F. 0.* 57: 69-84.

Gory G. et Jeantet R. 1986. La colonie de Martinets noir (*Apus apus* L) du Museum de Nîmes. Compte rendu de 19 années de baguage. *Bull. Soc. Ent. Sc. Nat. Nîmes et Gard* 57: 46-52.

Koskimies J. 1950. The life of the swift, *Micropus apus*, in relation to the weather. *Ann. Acad. Sc. Fen.* 4, Biol. N°15 (A): 151.

Lack D. 1956. Swifts in a tower. *London, Methuen & Co Ltd.*

Lebreton J. D., Burnham K. P., Clobert J. and Anderson D. R. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monograph.*

Malacarne G., Palomba I., Griffa M., Castellano S. and Cucco M. 1989. Quantitative analysis of differences in the vocalizations of the Common Swift *Apus apus* and the Pallid Swift *Apus pallidus.Avocetta* 13: 9-14.

Malacarne G. and Cucco M. 1990. Shifts in sound features of the duetting pallid swift *Apus pallidus. Boll. Zool.* 57: 51-53.

Malacarne G., Cucco M. and Camanni S. 1991. Coordinated visual displays and vocal duetting in different ecological situations among Western Palearctic nonpasserine birds. *Ethol. Ecol. Evol.* 3: 207-219.

Owen D. F. 1955. Coeloptera taken by swifts (*Apus apus* L.). *J. Soc. Brit. Entomology* 5:3

Perrins C. M. 1971. Age of first breeding and adult survival rates in the swift. *Bird Study* 18: 61-70.

Richard J.-P. 1991. Sound analysis and synthesis using an Amiga Micro-computer. *Bioacoustics* 3: 45-60.

Avocetta N° 17: 147-156 (1993)

Patterns of food allocation between parent and young under differing weather conditions in the Common Swift (*Apus apus*)

THAIS L.F. MARTINS and JONATHAN WRIGHT

Edward Grey Institute of Field Ornithology, Department of Zoology,
South Parks Road - Oxford OX1 3PS, England
Department of Zoology, Dowing Street - Cambridge CB2 3EJ, England

Abstract – Brood sizes were manipulated to promote different levels of parental effort in the Common Swift (*Apus apus*). The two years in which these brood size manipulations were carried out differed with regard to weather conditions. Data were collected on a visit by visit basis to reveal changes in parental and chick body mass, the mass of prey delivered and the estimated mass of parental self-feeding. This provided a powerful method for testing hypotheses regarding parental investment decision concerned with optimal allocation strategies between parents and young and how these can be affected by resource conditions. When weather conditions were "good" (warmer and sunnier), parents did not have to lower their own self-feeding to increase the amount of food delivered to larger broods as they did when conditions were "bad" (cold and wet). Only in "good" weather conditions did parents suffer no mass loss as a result of increased parental effort, and incur no increased costs from raising larger broods. In addition, "good" weather conditions meant that fledging mass in larger broods was similar to that in smaller broods, which suggests that a reduction in the survival chances of fledglings from larger broods only occurred in "bad" weather conditions. The differential allocation responses shown in both years are discussed in terms of parental strategies to cope with increased brood demands.

Introduction

The trade-off between present and future reproductive success is central to life-history theory (Williams 1966, Charnov and Krebs 1974, Stearns 1976, Ricklefs 1977, Calow 1979). However, such trade-offs have proved difficult to quantify in the field, and in fact positive relationships between reproductive performance and adult survival are often recorded instead (Kluyver 1971, Bryant 1979, Högstedt 1981, Smith 1981, Ricklefs and Hussel 1984), which usually reflects inherent differences in individual quality (Perrins and Moss 1975, Pettifor *et al.* 1989). It is widely accepted that the effect of this phenotypic variation in individual quality should be overcome using experimental manipulation (Askenmo 1979, De Steven 1980, Bell 1984, Partridge and Harvey 1985,1988, Nur 1988, Smith *et al.* 1988, Orell and Koivulla 1988, reviews in: Reznick 1985, Reznick *et al.* 1986, Bell and Koufopanou 1986, Nur 1988). However, even experimental studies are not problem free, either because monitoring adult survival and recruitment of young has its limitations or because environmental conditions can affect reproductive costs. If conditions are favourable, costs are likely to be small or absent, whilst if conditions are harsh costs may be high (Nur 1988). Therefore, assessments of costs of reproduction over a number of seasons may be necessary in order to infer a selective consequence in terms of life-history.

It is normally assumed that parental investment decisions operate in the long-term with parents trading levels of care in the present breeding attempt against breeding success in the future (Trivers 1972). This is probably because most theoretical treatments of parental investment deal with the problem as one of evolutionary trade-off and there is a tendency to ignore the possibly that such trade-offs can operate over behavioural time-scale within a breeding attempt (Lima and Dill 1990, see also Martins and Wright 1993a,b). One example of a behavioural trade-off which can be expected to have life-time consequences is the way in which breeding birds must divide the food they gather between themselves and their offspring. Benefits gained from delivering food to the young have to be traded-off against the need of the parent to feed and maintain its own physical contition, and retain a chance of survival to future breeding attempts (reviews in: Partridge and Harvey 1985 1988, Reznick 1985, Nur 1988) or retain future

---

Accepted 20 December, 1993

fecundity (Gustafsson and Pärt 1990). The parental allocation of resources should therefore be optimized between present and future reproductive attemps so as to maximize life-time reproductive success (Kacelnik and Cuthill 1990).

By manipulating brood size and therefore the levels of parental effort in the Common Swift (*Apus apus*) we aimed at investigating the resulting changes in parental foraging strategy. The allocation of food between parent and young was directly assessed on a visit by basis using the load mass delivered, the calculated energic cost of the feeding trip and the changes in adult mass during that trip. Conditions differed considerably in the two years in which brood size manipulations were carried out in the swift study colony. This offered an unique opportunity to look at the effects of resource availability on the patterns of parental investment and food allocation. The aim of this paper is therefore to investigate the changes in foraging strategy of parents feeding manipulated brood sizes under different conditions and to evaluate the associated costs in terms of adult body mass loss.

Methods

This study was carried out in 1988 and 1989 in the nest-box colony in the University Museum tower in Oxford, U. K. This swift colony is well established and contains over 60 breeding pairs and was the site of David Lack's original work on the breeding of common swifts (Lack 1954, 1956, 1964, 1968; Lack and Lack 1951, 1952). The Common Swift is a long-lived aerial insectivore that spends all of its time outside the nest flying and has no post-fledging care. It is therefore an excellent species for the study of costs of reproduction during the nestling phase. Data for the 1988 breeding season, a season in which resources were limiting, was presented separately elsewhere (Martins and Wright 1993a, b). The data analyses presented here are concerned with investigating the year effect in a combined years data set.

Adults were sexed by identifying the females during laying. Due to a high sensitivity to disturbance at this stage, females were marked on the head with hydrogen peroxide using a long brush (Malacarne and Griffa 1987). Parent birds were caught in the nest boxes at the end of each breeding season when they were weighed and given sex-specific colour rings. In both years, when chicks were at the age of five days, brood sizes of one to three were randomly assigned to 15 nests in roughly equal numbers, such that every chick was reared in a nest other than its original nest (Table 1). In 1988, due to a prolonged cold spell, in two of the five nests with an experimental brood size of three, one chick died early in the nestling phase and these nests were not included in any of the following analyses (but see Martins and Wright 1993b). There were no statistically significant differences between the three groups before the manipulation in either lay-date or hatch-date for either of the two breeding seasons (1988: $F_{2,10}=0.32$, $P=0.73$; $F_{2,10}=0.32$, $P=0.74$; 1989: $F_{2,12}=0.13$, $p=0.88$; $F_{2,12}=0.04$, $P=0.96$ respectively). It should be noted that no significant effects of original clutch size were found in any of the preliminary tests (i.e. $P>0.50$) and it was therefore not included in any of the following analyses.

Table 1. The brood size manipulation in 1988 and 1989 with number of nests used (n).

	MANIPULATED BROOD SIZE		
	1	2	3
1988			
mean lay-date	21.0	19.6	19.3
mean hatch-date	43.6	42.8	41.3
n	5	5	3
1989			
mean lay-date	20.0	21.0	20.3
mean hatch-date	42.2	42.2	41.8
n	5	4	6

A system of electronic balances (Ohaus Port-O-Gram, model c501, 500g capacity, 0,1g accuracy, Ohaus Scale Europe, Cambridge, U.K.) linked to a BBC model B Microcomputer through a switching device (Smart switch, model V. 24, Inmac, U.K.) were used in both years to collect data on parental visits during the nestling period (for detailed methods see, Martins and Wright 1993a). In 1988, adults were weighed each day when feeding chicks on the balance, making it possible to sex the birds on most days on the basis of differences in body mass between the parents. In 1989, at hatching, small magnets were glued to one parent's colour ring and a system of micro-switches (Martins 1992) and magnet-detectors (Hall-plate detector: for specifications see Stevens 1984) were used to record visits to the nest and to sex the visiting parent bird. All chicks were individually weighed every day by hand using the same balance set-up. Analyses concerning mean chick masses and mean mass of the heaviest chick refer to the period after 12 days of age (i.e. after the exponential growth phase and at the mass asymptote; Lack 1956). Using this set-up, parental mass on arrival and departure could be derived from the extra mass of the nest during a visit, and the differences in these corresponded to the mass of the food bolus brought to the chicks. Faecal sacs were not considered in these calculations since they are usually left in the nest by the adults (Lack and Lack 1952). Using the data in this form, other variables could also be derived, such as time spent in the nest-box, the length of time of each feeding trip (i.e. time of round trip) for each sex and the parental mass gained or lost during these feeding trips.

In order to calculate how much each parent fed itself (in terms of grams of fat when away from the nest, an estimate was needed of the energy spent per hour of foraging flight. Since, 1 BMR costs 1.57 KJ per hour, with active flight estimated at 12 BMRs, this gives a cost of flight in swifts of 18.84 KJ per hour (Dolnik and Kinzhewskaja 1980). Although energy can be obtained from other forms of metabolic products, it is usually accepted that birds primarily use fat (Berger and Hart 1974, Griminger 1986). So, if the amount of metabolizable energy obtainable from a fram of fat is believed to be around 37.7 KJ per gram (Blem 1990), dividing by the cost of flight means that a swift could fly for two hours using one gram of fat, using 1.38 x 10-4 grams of fat per second in active flight.

"Self-feeding" can then be calculated as the total energetic cost of that flight trip plus the adults body mass change for that trip (as in equation 1).

$$S=(T*C*1.57/3600*E)+W \qquad \text{(eq.1)}$$

where S is the estimated amount of self-feeding in g;
T is time of a foraging trip in seconds;
C is the cost of flight in BMRs;
E is the energy obtainable from a gram of food in $KJ*g^{-1}$; and 1.57/3600 is the cost of 1 BMR in swifts in $KJ*sec^{-1}$. Self-feeding is therefore not the mass of insects in the gut, but the mass of fat assimilated. The rates of assimilation of insects as energy stores and of convertion of fat into energy are not known for swifts, but are assumed in this paper to be the same for every bird. Therefore, costs of assimilating food into energy and vice-versa are not included here. The use of such a method for estimating self-feeding are not of consequence here and are fully discussed elewhere (Martins 1992, Martins and Wright 1993a).

It is important to emphasise that the random assignment of brood sizes as an experimental design and the form of data collection used here standardises for any effect of weather on foraging conditions between brood sizes within the same year. The effect of weather conditions on the foraging strategies can therefore be assessed by contrasting the two breeding seasons, 1988 and 1989.

For ease of analysis and to avoid pseudo-replication (Hulbert 1984), multiple analysis of variance (MANOVAS) were performed on the averages per bird or per nest as appropriate. It is important to point out that for all measures of parental effort (per bird) and chick mass (per nest), the within subject variation (i.e. within nests and birds) are not of concern here and therefore averages are an unbiased statistics to use.

MANOVAS were performed using the GLM procedure from the SAS system statistical package (SAS Institute Inc, Cary, NC). Contrasts were performed within each model and F-values calculated by dividing the mean sum of squares for the contrast of interest and the mean sum of squares for the error in the model. MANOVAS were performed on variables for the effect of brood size, year and the interaction between these two factors. Statistical contrasts for each overall step up in brood size, linear and quadratic terms, and also between years for each brood size were performed. In the same model, within year contrasts were also performed on the overall brood size effect and whether this effect was linear or quadratic. For brevity, such contrasts are presented only if they are of particular interest.

The meteorological data were provided by the School of Geography, Oxford University and were recorded at the Radcliffe Meteorological Station in Oxford.

Results

Weather Conditions

A summary of the weather conditions during the swift nestling periods in 1988 and 1989 is given in Table 2. All analyses were performed on the meteorological data for the period from the first chick hatching until the last fledging day of experimental nests in both years. The nestling rearing period in 1988 was significantly colder, less sunny and more windy than 1989.

The mean maximum temperature for the years of 1947 to 1990 (n=44) was calculated for the equivalent period (i.e. when adults swifts should have been providing food to the chicks, in this case estimated as the period between the 7th June and 31st July) is given in Fig. 1. The average maximum temperature for all years (excluding 1988 and 1989) was 20.75 ± 3.70 °C (mean ± s.d.). The years of 1988 and 1989, shown in the graph, are both within one standard deviation of the mean. These two years therefore represent the two extremes of the distribution of mean maximum temperatures for swift nestling feeding periods in these past 44 years.

Table 2. Summary of the weather conditions during the swift nestling periods in 1988 and 1989. Rainfall, maximum and minimum temperature refer to the period 09:00 - 03:00 GMT. Wind speed and humidity are collected at 09:00 GMT. Sample sizes are 49 and 53 days for 1988 and 1989 respectively.

	1988		1989			
	mean	se	mean	se	t	P
maximum temperature (°C)	19.05	0.36	24.08	0.56	-7.43	<0.001
minimum temperature (°C)	11.19	0.30	13.16	0.37	-4.03	<0.001
rain (mm)	2.07	0.60	0.98	0.38	1.54	0.125
sunshine (hours)	4.70	0.64	8.97	0.61	-4.79	<0.001
humidity (%)	78.61	1.67	69.24	1.66	3.97	<0.001
wind speed (knots)	9.65	0.69	7.96	0.74	2.04	0.044

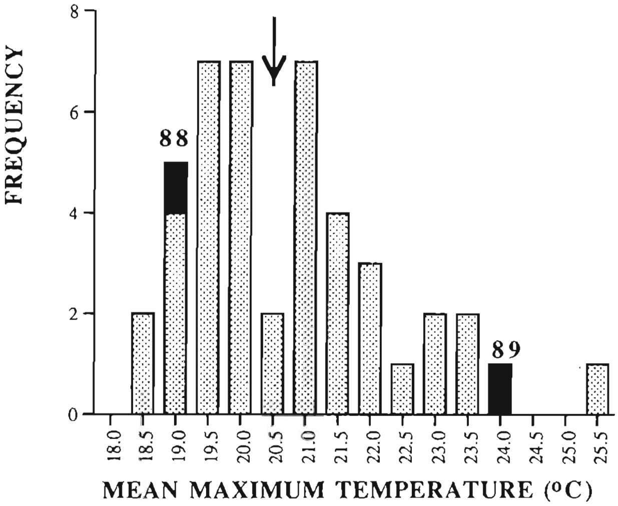


Figure 1. Mean maximum temperature distribution for the months of June and July (when swifts usually have chicks in the nest) for the years from 1947 to 1990 (n=44). The position for 1988's and 1989's mean maximum temperature are shown in dark. The arrow points at the average mean maximum temperature for these 44 years (88 and 89 excluded).

Parental Effort

Nests with more young were visited more often by the parents (Fig. 2A:$F_{2,44}$=4.69, P=0.014). Overall, the number of visits was the same for the two years ($F_{1,44}$=0.08, P=0.782), and the brood size effect was not significantly different between years (interaction term: F2,44=1.05, P=0.357). When broods of different sizes were contrasted overall, it becomes clear that the brood size were effect was the result of a significant increase in visits between brood size 1 and 2 only (contrast 1 vs 2: F:$_{1,44}$=8.26, P=0.006; contrast 2 vs 3: $F_{1,44}$=0.19, P=0.667; linear contrast term $F_{1,44}$=4.88, P=0.032). The increase in number of visits within 1988 was significant (contrast brood size within 88:$F_{1,44}$=4.66, P=0.014) and although it was not quadratic in form it approached significance (linear contrast for 88:$F_{1,44}$=3.68, P=0.061; quadratic contrast for 88:$F_{1,44}$=3.60, P=0.064). For 1989, there was no effect of brood size on the number of visits (contrast brood size within 89:$F_{1,44}$=0.79, P=0.458).

Overall, mean load mass increased linearly with brood size (Fig.2B:$F_{2,42}$=4.24, P=0.021; contrast 1 vs 2:$F_{1,42}$=0.07, P=0.791; contrast 2 vs 3:$F_{1,42}$=6.05, P=0.018; linear contrast term: $F_{1,42}$=7.14, p=0.011) and loads were generally larger in 1989, but the year effect only approached significance ($F_{1,42}$=3.69, P=0.061). The interaction term indicates that the increase in the load size in response to an increase in brood size was not significantly different between years ($F_{2,42}$=0.007, P=0.930). Within years, the increase in the load mass was not significant in 1988 and it approached significance in 1989 (contrast brood size within 88:$F_{2,42}$=1.82, P=0.174; contrast brood size within 89:F2.42=3.01, P=0.060). However, only for 1989 the linear contrast was significant (linear contrast within 89:$F_{1,42}$=5.30, P=0.026).

Food delivery rate also increased significantly with brood size (Fig.2C:$F_{2,42}$=7.67, P=0.001; linear contrast term $F_{1,42}$=14.61, P<0.001). Al-though there was a consistent trend for greater food delivery rates in 1989, this was not statistically significant when years were compared ($F_{1,42}$=2.47, P=0.124), and the interaction between brood size and year was not significant ($F_{2,42}$=3.73, P=0.691). Within years, there was also an increase in the food delivery rate with brood size (contrast brood size within 88:$F_{2,42}$=4.30, P=0.020; contrast brood size within 89:$F_{2,42}$=3.73, P=0.032), which was linear in both years (linear contrast for 88: $F_{1,42}$=7.71, P=0.008; linear contrast for 89:$F_{1,42}$= 7.45, P=0.009).

Food delivery per chick (g*day-1) decreased significantly with brood size (Fig.2D:$F_{2,22}$=37.01, P<0.001; linear contrast term: $F_{1,22}$=68.50, P<0.001). Although there was a tendency for food delivery per chick to be higher in 1989, this difference is not statistically significant ($F_{1,22}$=2.77, P=0.110). Also, the interaction term indicates that the response to brood size was not significantly different between years ($F_{2,22}$=0.46, P=0.638). The decrease in the food delivery per chick was significant and linear in both years (contrast brood size within 88:$F_{2,22}$=20.73, P<0.001; contrast brood size within 89:$F_{2,22}$=16.96, P<0.001; linear contrast for 88: $F_{1,22}$=35.73, P<0.001; linear contrast for 89: $F_{1,22}$=33.15, P<0.001).

Chick mass

Mean chick mass decreased with manipulated brood size (Fig. 3A:$F_{2,22}$=12.83, P<0.001; linear contrast term: $F_{1,22}$=24.89, P=<0.001), and tended to be higher in 1989 than in 1988, with this difference closely approaching significance ($F_{1,22}$=4.21, P=0.052). Although mean chick mass tended to decrease with brood size in 1988 and not in 1989, the interaction term was not significant (interaction term: $F_{2,22}$=2.65, P=0.093). However, when years are contrasted within

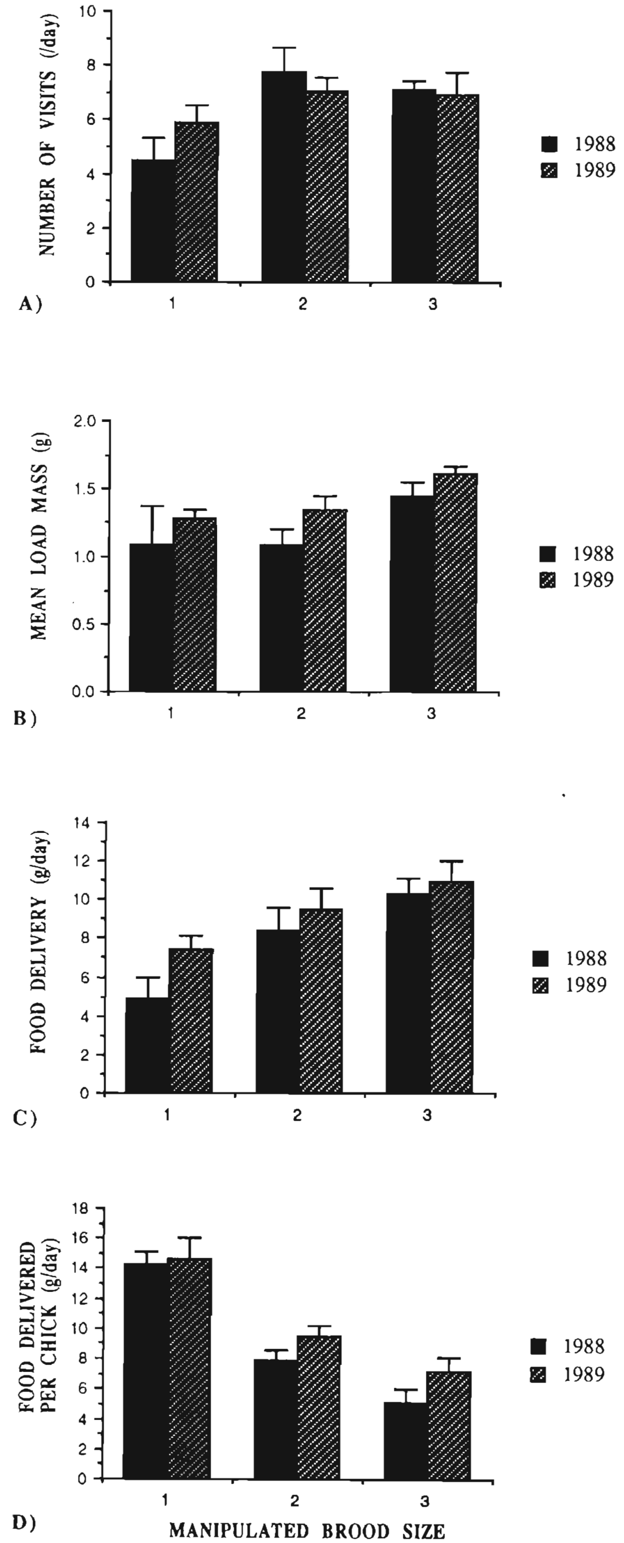


Figure 2. The effect of manipulated brood size on mean parental effort in both years (+SE) in terms of: A) number of visits per day; B) load mass delivered; C) food delivered per day per bird; and D) food delivery per chick per day.

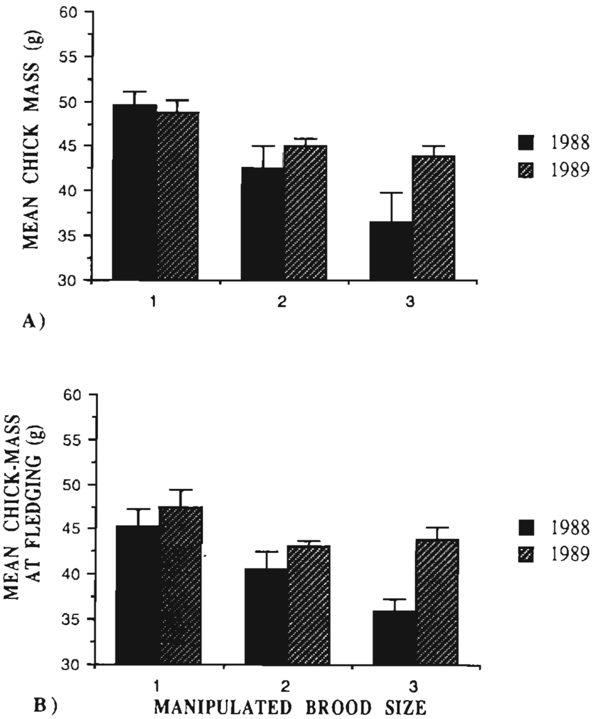


Figure 3. The effect of manipulated brood size in both years (+SE) on: A) mean chick mass; B) mean fledging mass.

brood sizes, mean chick mass was significantly higher in 1989 than in 1988 for broods of three, but not for brood size 1 and 2 (contrast year within brood size 1: $F_{1,22}$=0.11, P=0.738; contrast year within brood size 2: $F_{1,22}$=0.88; P=0.357; contrast year within brood size 3: $F_{1,22}$=7.73, P=0.011). Within years, the brood size effect was present for 1988 only (contrast brood size within 88: $F_{2,22}$=11.65, P<0.001; contrast brood size within 89: $F_{2,22}$=2.35, P=0.119).

Fledglings

Mean fledging mass decreased with manipulated brood size (Fig. 3B: $F_{2,22}$=6.80, P=0.005; linear contrast term: $F_{1,22}$=13.05, P<0.001), and mean fledging mass was higher in 1989 than in 1988 ($F_{1,22}$=7.98, P=0.010). The interaction term was not significant, showing that the effect of brood size was similar in both years ($F_{2,22}$=1.54, P=0.237). However, when years were contrasted within brood sizes, chicks from broods of three were found to fledge at a significantly higher body mass in 1989 than in 1988 (contrast year within brood size 3: $F_{1,22}$=8.63, P=0.007). Within years the brood size effect was present and linear for 1988 only (contrast brood size within 88:$F_{2,22}$=5.71, P=0.010; linear contrast for 88 only: $F_{1,22}$=11.13, P=0.003; contrast brood size within 89: $F_{2,22}$=1.77, P=1.193).

Food allocation between parent and young on a visit by visit basis

As can be see from Figure 4 the trend found in 1988 for parents to allocate less to themselves with an increase in brood size (Martins and Wright 1993a) was also present to a lesser extent in 1989. However, mean self-feeding in 1989 was not significantly different for broods of different sizes ($F_{2,17}$=0.42, P=0.666). When years were combined, no brood size effect was found on the mean self-feeding (Fig. 4:$F_{2,32}$=1.48, P=0.243), and there was no significant effect of year ($F_{1,32}$=1.10, P=0.302) and no significant interaction effect between the two ($F_{1,32}$=0.15, P=0.865). In fact there was a tendency for a linear decrease in self-feeding for years combined, but this trend also not significant (linear contrast term: $F_{1,32}$=2.95, P=0.096). Within years, the effect of brood size was also non-significant (contrast brood size within 88:$F_{2,32}$=0.90, P=0.418; contrast brood size within 89: $F_{2,32}$=0.62, P=0.542).

In 1989, the negative relationship between mean self feeding and mean load mass was significant (Fig. 5: r^2=0.088, P=0.168), suggesting that in that year birds did not consistently trade-off the food delivered with their own feeding. This result also holds when the data are analysed within birds. Regressions of load mass on self-feeding were performed for each bird separately, and a MANOVA was performed on the slopes from the regression equations. The constant term was not significant ($F_{1,15}$=0.37, P=0.552) showing that the slopes were not different from zero, i.e. that there was no overall relationship between load mass and self-feeding and that there was no effect of brood size ($F_{2,15}$=0.28, P=0.759).

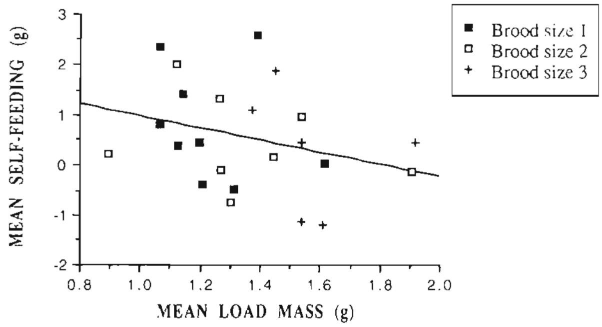


Figure 4. The effect of manipulated brood size on mean self-feeding by parents (+SE) in 1988 and 1989.

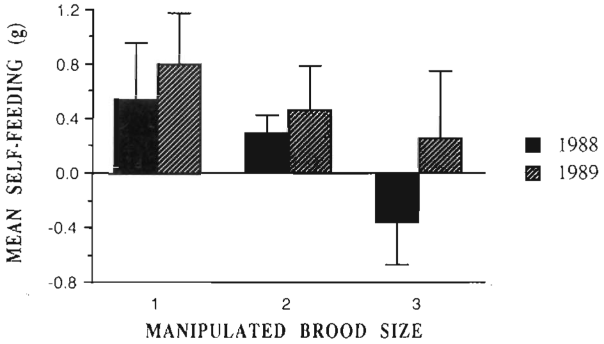


Figure 5. The relationship between mean load mass delivered and mean self-feeding over the whole nestling period in 1989, with the three manipulated brood sizes. Points are means per bird.

Mean total amount of food collected also did not differ significantly for the three different brood sizes ($F_{2,33}$=0.02, P=0.980). Also, although there was an increase in the total amount of food collected between years this difference was not statistically significant ($F_{1,33}$=1.76, P=0.193). Within years, total amount of food collected was also non-significant for different brood sizes (contrast brood size within 88: $F_{1,33}$=0.02, P=0.981; contast brood size within 89: $F_{1,33}$=0.14, P=0.868).

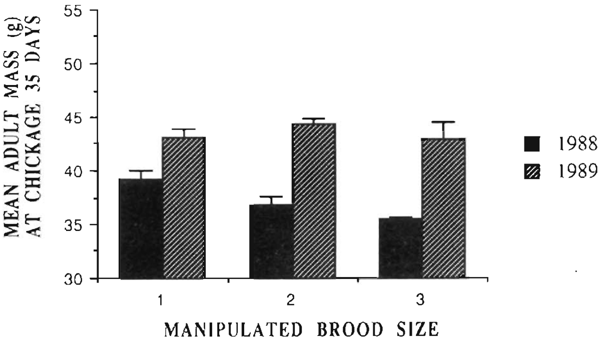


Figure 6. The effect of manipulated brood size on mean adult mass (+SE) in 1988 and 1989.

Adult body mass

Mean adult body mass at the end of chick feeding was also not significantly different for manipulated brood sizes (Fig. 6: $F_{2,38}$=1.47, P=0.244), but parents in 1989 were significantly heavier than parents in 1988 ($F_{1,38}$=48.9, P<0.001). Although the interaction was not significant ($F_{2,38}$=2.07, P=0.140), contrasts between years for each brood size were significant (contrast year within brood size 1: $F_{1,38}$=8.19, P=0.007; contrast year within brood size 2: $F_{1,38}$=23.92, P<0.001; contast year within brood size 3: $F_{1,38}$=18.15, P<0.001) showing that within each one of the brood sizes parent birds weighed more in 1989 than in 1988. Therefore, an increase in the parental effort resulted in decreased body mass in only one of the breeding seasons.

There was no brood size effect in parental body mass at fledging when years were combined ($F_{2,31}$=0.66, P=0.525), or a year or an interaction effect ($F_{1,31}$=0.54, P=0.467; interaction term: $F_{2,31}$=0.69, 9=0.51). Within years the effect of brood size on adult body mass at fledging was also non-significant (contrast brood size within 88:$F_{2,31}$=1.81, P=0.180; contrast brood size within 89: $F_{2,31}$=0.03, P=0.969). Therefore, at the end of each season, parent swifts of both sexes weighed the same as each other whatever brood size they raised.

Discussion

Parental effort and brood size

Over the two years, the brood size manipulation created greater food delivery per day in nests with more young. In 1989, when conditions were better in terms of swift feeding, increases in the food delivery rates to larger brood sizes were mostly due to increases in the load size delivered between broods of 2 and 3. This result differs from 1988 (Martins and Wright 1993a), in which a similar increase in food delivery with brood sizes was mostly due to an increase in number of visits between broods of 1 and 2. It is interesting that the same expected linear increase in food delivery rates with brood size (Bryant and Gardiner 1979, Winkler 1987, Montgomerie and Weatherhead 1988; see reviews in Klomp 1970, Nur 1984a, 1988) ocurred in both years, but was achieved in alternative ways as a result of different combinations of increases in the number of visits and in the load mass. This suggests that according to resource conditions, differential parental foraging strategies may exist with regards to how the step-up in feeding effort is achieved in response to increases in brood size, and also that the resulting level of sustained effort seems to be determined by conditions. However, in both years, overall increases in food delivery to the largest brood size seems to have been achieved mainly by increasing the size of the loads delivered (see also analyses in Martins and Wright 1993a). This strategy of returning to the nest only when a large load has been gathered, suggests that parent swifts raising larger broods could be conserving energy by reducing the number of trips and so reducing travel costs. Raising larger broods, even under good conditions, might still be energetically demanding. Further evidence that this might be true comes from the trade-off between load mass and prey quality for boluses delivered to the larger brood sizes in 1989 (Martins 1992, Martins and Wright in prep.).

Although aerial insect prey must have been more abundant in 1989, food delivery rates were still not proportional to the number of chicks in the nest, and delivery rates per chick decreased with brood size. This is the expected pattern seen in many studies (Sibly and Calow 1983, Nur 1984a, b, 1988; Wright and Cuthill, 1990a, b), which reflects parental investment trade-off decision between parental care and future survival to future reproductive attempts.

Chick mass

In 1989, chicks in broods of three were not only as heavy as chicks from other brood sizes during the nestling period, but they also fledged at a similar body mass. Higher fledging masses in that year might have been expected to increase subsequent survival chances and future recruitment rates (Virolainen 1984, Alatalo and Lundberg 1989). This result differs from 1988, when broods of three, might be expected to have had reduced survival chances due to lower fledging mass (Martins 1992, Martins and Wright 1993a). There fore, parents raising broods of three in 1989 probably produced more rescruits into the future breeding population than parents raising one or two chicks (although note that due to the manipulation these chick were not related to them genetically). The reverse was probably true for broods of three in 1988. Therefore, in years with good feeding conditions, such as in 1989, raising maximum brood-sizes (i.e. three chicks) could enhance a parent's life-time reproductive success, particularly if it did not decrease the parent's chances of future survival. Whilst in poor years, such as 1988, the best strategy may be to raise only two chicks, brood reduction happening then as an adaptive response to conditions (see Martins and Wright 1993b).

Adult body mass and the allocation of food

In 1989, adult swifts raising larger brood sizes did not lose body mass . As a result, they probably did not suffer any increased risk of predation from their higher levels of parental effort as might have occurred in 1988 (Martins and Wright 1993a, b). Therefore, the patterns of parental body mass loss presented here suggest that the costs, from the possible increase in the risk of predation as parental care levels increase, are more likely to happen in years with poor feeding conditions (Martins and Wright 1993a, 1993b).

The patterns of adult body mass loss seem to be due to the differential allocation strategies used by parent birds during the course of the two different nestlings season. Under good resource conditions, the trade-off in food allocation between parent swifts and their young was not as sensitive to the value of the brood as it was under poor conditions. In 1988, the effect of brood size was evident in the way that parent swifts feeding larger broods did so at the expense of their own feeding. The subsequent low parental body mass resulted in periods of exclusive self-feeding in the nestling period and in extreme cases this led to brood reduction (Martin and Wright 1993a, b). Current models of food allocation between parent and young (Kacelnik 1984, Kacelnick 1988, Kacelnick and Cuthill 1990) predict that under very controlled resource conditions optimal allocation is dependent on both the value of the brood and on the rate at which food was being artificially delivered. In the case of abundant food resources, such as in 1989, variables such as the state of parents and young might become more important in predicting the optimal allocation decision. One possible scenario in the situation of food abundance is that parents would adjust their intake to balance their expenditure, whilst delivering the excess to the young. We have shown here that under good conditions the value of the brood is not a good predictor of the way parent swifts allocate their food and that in such years parents did not seem to incur major costs in raising larger brood sizes.

The lack of a consistent trade-off between self-feeding and load in 1989 is also interesting when considering that there was no brood size effect in the total amount of food collected by parent birds in that year. It seems that in 1989, although total food collected per foraging bout was also limited, this may not have been due to conditions but some other constraint such as the size of throat pouch or transport costs (Cuthill and Kacelnik 1990).

Parental strategies and associated costs in coping with larger brood demands

Work done on food allocation in parent swifts has so far shown that delivering larger loads seems to be the first strategy used by parent swifts to increase delivery to larger brood sizes and that this is probably due to the lower energetic costs associated with this strategy (Martins and Wright 1993a). This strategy was also evident in the trade-off between the size and the quality of loads delivered, even during the good feeding conditions in 1989 (Martins 1992, Martins and Wright in prep.) When conditions deteriorate, differential allocation between parent and young probably becomes necessary and/or more pronounced, thus resulting in loss of parental body mass. However, if conditions remain poor for longer, and if parents have reached a certain "threshold" in body mass then parents swifts might tend to allocate to themselves mainly and eventually even stop chick feeding, which may or may not, result in brood reduction, depending on the duration of the bad spell (Martins 1992, Martins and Wright 1993a, b).

In 1989, parent swifts showed no resulting decrease in their own chances of survival to breed in the future and no apparent increase in the short-term risk of predation, as in 1988 (Martins and Wright 1993a). So, it seems that foraging conditions appear to determine how big a cost there is to raising a brood of three chicks. It has been also found for other species that fledging success (Virolainen 1984, Alatalo and Lundberg 1989) and/or parental survival (see Högstedt 1981, Murphy and Haukioja 1986) may be also improved in more favourable conditions.

It is possible that a relaxation in the selective disadvantage of rearing a larger brood makes the cost of reproduction less important with respect to the evolution of clutch size. However, years like 1989 are not very common. It is therefore expected that reproductive years such as 1988 would constrain the system by discriminating against overly large brood sizes. However, it is the feeding strategies used by parents to cope with changes in food conditions that limit the amount of food that can be brought to the chicks. In 1988, the need to increase the amount of food delivered was accomplished by trading-off the amount of food that parent were allocating to themselves on a visit-by-visit basis. In 1989, this trade-off between load and self-feeding was relaxed. So, are parent swifts limited by the amount of food that they can gather for the chicks (Lack 1947, 1968), because they are ultimately limited by how far they can trade-off their own feeding with the load they bring to the chicks on a visit-by-visit basis? Data on food allocation in swift so far seem to suggest that this short-term behavioural decision, in terms of allocation in future and presente reproductive attempts, seems to determine the amount of parental effort expended on a single reproductive attempt thus restricting the number of chicks that can be raised. However, this trade-off is relaxed when resources are abundant permitting larger brood sizes to be raised without major costs.

Acknowledgments - for help in BBC computer programming, thanks to David Nash and Robin McCleery, for discussion and comments, thanks to Chris Perrins, Alasdair Houston, Alex Kacelnik, Ben Hatchwell, Gareth Jones and Liz Brown. TM was supported by a CNPq scholarship (Brazil) and an Overseas Research Scheme grant, JW was funded by the AFRC Unit of Ecology & Behaviour in Oxford.

Resumo - Manipulações do tamanho de ninhada foram realizadas para promover diferentes níveis de esforço parentalo Andorinhão Preto (*Apus apus*). Nos dois anos nos quais esta manipulação foi realizada condições climáticas diferiram grandemente. Os dados foram analisados a cada evento de forrageamento em relação `a mudanças na massa corporal do adulto visitante e dos filhotes, no massa da bolota de alimento trazida para os filhotes e na massa estimada da quantidade de alimento ingerida pelo mesmo adulto visitante (i.e. "self-feeding"). Tal análise possibilitou o teste de hipótese sobre decisões de investimento parental relativas `a estratégias de alocamento ótimo entre pais e filhotes e como estas podem ser influenciadas por diferenças em recursos alimentares. Durante o ano de boas condições climáticas (quente e ensolarado), os adultos não precisaram reduzir a quantidade de alimento coletada para si mesmos para aumentar a quantidade de alimento trazida para as ninhadas maiores como demonstrado anteriormente para anos de condições climáticas ruins (frio e chuvoso). Adultos com ninhadas maiores também não sofreram nenhuma redução de massa resultantes do aumento no esforço parental expendido e aparentemente não sofreram nenhum custo em manterem ninhadas maiores. Além disso, boas condições climáticas possibilitaram que a massa dos filhotes ao deixarem ninhos em maiores ninhadas fosse similar `a daquelas provenientes de menores ninhadas sugerindo a não redução nas chances de sobrevivência de filhotes saídos de ninhadas maiores. As respostas diferenciais de alocamento de alimento demonstradas nos dois anos são discutidas em termos de estratégias parentais usadas para alimentar ninhadas maiores.

References

Alatalo R.V. and Lundberg A. 1989. Clutch size of the pied flycatcher (*Ficedula hipoleuca*) - an experiment. *Ornis Fennica* 66:15-23.

Askenmo C. 1979. Reproductive effort and return rate of the male pied flycatcher *Amer. Nat.* 114:748-753.

Bell G. 1984. Measuring the cost of reproduction. I. The correlation structure of the life table of a rotifer. *Evolution* 38:300-313.

Bell G. and Koufopanou V. 1986. The cost of reproduction. In: Dawkins R. and Ridley M. Eds. Oxford Surveys in Evolutionary Biology. *Vol.3. Oxford University Press, Oxford.*

Berger M. and Hart J.S. 1974. Physiology and energetics of flight. In: Farner, D.S. and King. J.R. Eds. Avian biology. *Academic Press, New York.*

Blem C.R. 1990. Avian energy storage. In: Power, D.M. Ed. Current Ornithology. *vol. 7. Plenum Press, New York.*

Bryant D.M. 1979. Reproductive costs in the house martin (*Delichon urbica*). *J. Anim. Ecol* . 48:655-676.

Bryant D.M. and Gardiner A. 1979. Energetics of growth in house martins (*Delichon urbica*). *J. Zool* . 189:275-304.

Calow P. 1979. The cost of reproduction - a physiological approach. *Biol. Rev.* 54:23-40.

Charnov E.L. and Krebs J.R. 1974. On clutch size and fitness. *Ibis* 116:217-219.

Cuthill I. & Kacelnik A. 1990. Central place foraging: a re-appraisal of the "loading effect". *Anim. Behav.* 40:1087-1101.

De Steven D. 1980. Clutch-size, breeding success, and parental survival in the tree swallow (*Iridoprocne bicolor*). *Evolution* 34:278-291.

Dolnik V.R. and Kinzhewskaja L.I. 1980. Time and energy budgets during the nest period in the swift (*Apus apus*) and swallows (*Delichon urbica, Hirundo rustica*). *Zool. Zh.* 59:1841-1851.

Griminger P. 1986. Lipid metabolism. In: Sturkie, P.D. Ed. Avian Physiology. *Springer Verlag, New York.*

Gustafsson L.. and Part T. 1990. Acceleration of senescence in the collared flycatcher *Ficedula albicollis* by reproductive costs. *Nature* 347:279-281.

Högstedt G. 1981. Should there be a positive or negative correlation between survival of adults in a bird population and their clutch size? *Am. Nat.* 118:568-571.

Hulbert J.H. 1984. Pseudoreplication and the design of field experiments in ecology. *Ecol. Monog.* 54:187-211.

Kacelnik A. 1984. Central place foraging in starlings (*Sturnus vulgaris*). Patch residence time. *J. Anim. Ecol* . 53:283-299.

Kacelnik A. 1988. Short-term adjustments of parental effort in starlings. In: Ovellet, H. Ed. XIX Congressus Internationalis Ornithologici, Ottawa, 1986. *University of Ottawa Press, Ottawa.*

Kacelnik A. and Cuthill I. 1990. Central place foraging in starlings (*Sturnus vulgaris*). II. Food allocation to chicks. *J. Anim. Ecol.* 59:655-674.

Klomp H. 1970. The determination of clutch size in birds: a review. *Ardea* 58: 1-124.

Kluyver H.N. 1971. Regulation of numbers in populations of great tits (*Parus m. major*). In: den Boer, P.J. and Gradwell, C.R. Eds. Dynamics of Populations. *Pudoc, Wageninger.*

Lack D. 1947. The significance of clutch size. *Ibis* 89:302-352.

Lack D. 1954. The natural regulation of animal populations. *Oxford University Press*, London.

Lack D. 1956. Swifts in a tower. *Chapman and Hall, London.*

Lack D. 1964. The significance of clutch size in swift and grouse. *Nature* 203:98-99.

Lack D. 1968. Ecological adaptations for breeding in birds. *Chapman and Hall, London.*

Lack D and Lack E. 1951. The breeding biology of the swift (*Apus apus*). *Ibis* 93: 501 546.

Lack D and Lack E. 1952. The breeding behaviour of the swift. *British Birds* 45:186-215.

Lima S.L and Dill L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68:619-640.

Malacarne G. and Griffa M. 1987. A refinement of the Lack's method for swift studies. *Sitta* 1: 175-177.

Martins T.L.F. 1992. The cost of reproduction in swifts. D.Phil thesis. *University of Oxford, Oxford.*

Martins T.L.F. and Wright J. 1993a. On the cost of reproduction and the allocation of food between parent and young in the common swift (*Apus apus*). *Behav. Ecol.* 4:213-223.

Martins T.L.F. and Wright J. 1993b. Brood reduction in response to manipulated brood sizes in the common swift (*Apus apus*). *Behav. Ecol. Sociobiol.* 32:61-70.

Montgomerie R.D. and Weatherhead P.J. 1988. Risks and rewards of the nest defence by parent birds. *Q. Rev. Biol.* 63:167-187.

Murphy E.C. and Haukioja E. 1986. Clutch size in nidicolous birds. in: Johnston, R.F. Ed. Current Ornithology. Vol 4. *Plenum Press, New York.*

Nur N. 1984a. The consequences of brood size for breeding blue tits. I. Adult survival, weight change and the cost of reproduction. *J. Anim. Ecol.* 53:479-496.

Nur N. 1984b. Feeding frequencies of nestling blue tits (*Parus caeruleus*): costs, benefits and a model of optimal feeding frequencies. *Oecologia* 65: 125-137.

Nur N. 1988. The cost of reproduction in birds: an examination of the evidence. *Ardea* 76:155-168.

Orell M. and Koivulla K. 1988. Cost of reproduction, parental survival and production of recruits in the willow tit Parus montanus. *Oecologia* 77:423-432.

Partridge L. and Harvey P. 1985. Costs of reproduction. *Nature* 316:20.

Partridge L. and Harvey P. 1988. The ecological context of life history evolution. *Science* 241: 1449-1455.

Perrins C.M. and Moss D. 1975. Reproductive rates in the great tit. *J. Anim. Ecol.* 44:695-706.

Pettifor R.A., Perrins C.M. and McCleery R. 1989. Individual optimization of clutch size in great tits. *Nature* 336:160-162.

Reznick D.N. 1985. The cost of reproduction: evaluation of the empirical evidence. *Oikos* 44:257-267.

Reznick D.N., Perry E. and Travis J. 1986. Measuring the cost of reproduction: a comment on papers by Bell. *Evolution* 40:1338-1344.

Ricklefs RE. 1977. On evolution of reproductive strategies in birds: reproductive effort. *Am. Nat.* 111 :453-478.

Ricklefs R.E. and Hussell D.J.T. 1984. Changes in adult mass associated with nestling cycle in the European starling. *Ornis Scand.* 15:155-161.

Sibly R. and Calow P. 1983. An integrated approach to life-cycle evolution using a selective landscape. *J. Theor. Biol.* 102: 527-547.

Smith J.M. 1981. Does high fecundity reduce survival in song sparrows? *Evolution* 35: 1142-1148.

Smith H.G., Kallander H., Fonlell K. and Ljungstrom M. 1988. Feeding frequency and parental division of labour in the double-brooded great tit *P. major.* Effects of manipulating brood size. *Behav. Ecol. Sociobiol.* 22:447-453.

Stearns S.C. 1976. Life-history tactics: review of the ideas. *Quart Review Biol* 51:3-47.

Stevens T.A. 1984. Food storing by marsh tits. D.Phil thesis. *University of Oxford, Oxford.*

Trivers R.L. 1972. Parental investment and sexual selection. In: Campbell B.Ed. Sexual selection and the descent of man. pp 136-179. *Aldine Press. Chicago.*

Virolainen M. 1984. Breeding biology of the pied flycatcher Fidedula hypoleuca in relation to population density. *Ann. Zool. Fennici* 21:187-197.

Williams G.C. 1966. Adaptation and natural selection. *Princeton University Press, NJ.*

Winkler D.W. 1987. A general model for parental care. *Am. Nat.* 130:526-543.

Wright J. and Cuthill I. 1990a. Manipulation of sex difference in parental care: the effect of brood size. *Anim. Behav.* 40:462-471.

Wright J. and Cuthill I. 1990b. Biparental care: short term manipulations of partner contribution and brood size in the starling, *Sturnus vulgaris. Behav. Ecol.* 1:116-124.

Avocetta N°17: 157-162 (1994)

Echolocation acuity of the Palawan Swiftlet (*Aerodramus palawanensis*)

CHARLES T. COLLINS(1) and RICHARD MURPHY(2)

(1)*Dept. Biological Sciences, California St. Univ., Long Beach CA 90840 USA*
(2) *The Cousteau Society, 870 Greenbrier Circle, Suite 402, Chesapeake VA 23320 USA*

Abstract – Echolocation acuity trials were conducted on Palawan Swiftlets (*Aerodramus palawanensis*) under natural conditions in Palawan, Philippine Islands. Detection of 3.2 mm diameter obstacles was significantly less than for 6.3 mm and 10 mm obstacles. These results are consistent with previous laboratory trials conducted on other swiftlets. They confirm that although echolocation is used for orientation in cave nesting and roosting areas it is unlikely to be effective in detecting their typically small (< 5 mm) food items.

Introduction

The ability to use echolocation or animal sonar is a widespread and well studied specialization among bats of the suborder Microchiroptera (Griffin 1958, Vincent 1963, Simmons *et al.* 1975, Busnell and Fish 1980). Among birds, echolocation is known only for the Oilbird (*Steatornis caripensis*) a unique cave nesting caprimulgid of northern South America (Griffin 1954, Konishi and Knudsen 1979) and most, if not all, of the widespread species of cave swiftlets (*Aerodramus* sp.) (Medway and Pye 1977) which occur from the western Indian Ocean islands of Mauritius and Reunion eastward to the islands of the southwest Pacific ocean (Sibley and Monroe 1990). The echolocation sounds utilized for orientation by birds are brief bursts or audible clicks lasting for a few milliseconds with a repetition rate of 3-20 clicks per second (Novick 1959, Griffin and Suthers 1970, Medway and Pye 1977, Fullard *et al.* 1993). The frequency range of these clicks is from 1-16 kHz (Medway and Pye 1977, Fullard *et al.* 1993) and there are no ultrasonic frequencies as typically found in microchiropteran pulses (Cranbrook and Medway 1965). The several tests of the acuity of echolocation in *Aerodramus* swiftlets (Griffin and Suthers 1970, Fenton 1975, Griffin and Thompson 1982, Smyth and Roberts 1983) have indicated that it is probably only utilized for flight orientation within caves where they nest and roost and not for foraging. However, most of the tests of swiftlet echolocation acuity have involved small numbers of individuals flying in laboratory conditions or a man-made mine shaft. We report here similar experiments conducted with the Palawan Swiftlet (*Aerodramus palawanensis*) under natural conditions in a large nesting and roosting cave.

Methods

These experiments were conducted in the underground river cave in St. Paul River Subterranean National Park, Palawan, Philippine Islands from 14-21 September 1990. The tests were conducted in a side channel off the main cave about 200 m from the entrance. This site was in constant total darkness. The test apparatus consisted of two bamboo poles erected next to the rock walls of the channel and connected by a lowerable rope, ca. 6 mm in diameter, stretched between pulleys. Suspended from this rope were 12 test obstacles consisting of 3.6 m lengths of nylon or manila rope 10 mm, 6.3 mm or 3.2 mm in diameter. The test obstacles (ropes) were centered 30 cm apart which allowed about another 30 cm space on either side between the outermost rope and the rock wall. Depending upon the tidal influenced water level in the cave the test obstacles stopped near the water surface or were about 50 cm above it. Small metal bells were attached to the bottom of each test obstacle as a further aid in detecting contact by a flying bird. Twenty four of twenty six separate trials with the several test obstacles were conducted between 16:45 and 20:00 when large numbers of swiftlets were returning to roosting sites in the cave; two additional trials were conducted from 10:20-11:30. Observations were

---

Accepted 30 December, 1993

made of individual swiftlets which either passed through the apparatus without striking a test obstacle (= a pass), struck a test obstacle (= a hit), or turned back before passing through but after having approached to within approximately 2 m of it (= a turn). Visual observations were made under two sets of conditions. The first was under very low light conditions achieved by reflecting a small incandescent headlamp beam off the ceiling above and slightly back from the test apparatus. This gave just enough light for the swiftlets to be seen and their performance quantified, but not enough illumination to allow them to decrease their utilization of echolocation. Elsewhere in the cave when either bright lights were used or when near the mouth of the cave and natural light was available, we noticed a clear decreased utilization of echolocation. Under these brighter light conditions, but not during the acuity trials, echolocation clicks were reduced in emission rate or were discontinued altogether (personal observation). The second method of observation entailed the use of a battery powered infrared light source to illuminate the test apparatus and the observation of the swiftlets by means of a night vision scope. Again, no diminution of echolocation clickemission rate seemed to occur under these conditions. In both observation conditions the birds' performance was thus thought to be strictly on the the basis of their ability to detect the test obstacles by echolocation alone.

We recorded a total of 1554 interactions in the form of 716 passes and hits and 838 turns in test and control observation periods. As all of the swiftlets observed were free-flying and unmarked the total number of separate individuals observed could not be determined; it is quite possible that observations were made of the same individual's performance on more than one day. Many thousands of swiftlets utilized the entire 8.2 km long underground river cave with some nests located at least 4 km from the cave mouth (Coleman 1981). A vastly smaller component of the population including those individuals with nests or roosts in the immediate vicinity of the test apparatus, or which used the channel to reach other more remote side chambers of the cave, were likely to have been observed during our experiments.

The taxonomy and identification of swiftlets, particularly in the field, is very confusing. Recent reviews of the Philippine Island swiftlets (Dickinson 1989, Sibley and Monroe 1990) indicate the presence in Palawan of a swiftlet which can be considered either as an endemic subspecies, *palawanensis*, of the widespread Mossy-nest Swiftlet *Aerodramus vanikorensis* (Dickinson 1989) or an endemic species *A. palawanensis* (Sibley and Monroe 1990). In light of several distinctive aspects of this swiftlet (Collins, unpublished) and until more definitive information is available, we follow Sibley and Monroe (1990) in giving *palawanensis* full species status. Our observations and prior field work by Coleman (1981) indicate that the swiftlets of the underground river are attributable to this species. This was further confirmed by comparison of museum specimens and a voucher specimen (#7391) housed in the ornithological collections of California State University, Long Beach. This specimen was one of a total of 19 swiftlets, randomly captured in the underground river cave, which were weighed, measured and examined before release, all of which seemed to belong to this single species (Collins, unpublished). Two other non-echolocating species, the Glossy Swiftlet, *Collocalia esculenta* and Pygmy Swiftlet, *C. troglodytes* were seen near the mouth of the underground river cave but were never seen to penetrate beyond the area of natural light (personal observation).

Echolocation acuity and obstacle avoidance were judged by the percent passes and hits of birds flying through the apparatus and also by means of a model formulated by Smyth and Roberts (1983) of a theoretical missile the same width as the wing span of the swiftlets traveling through the test apparatus. This model determines that the probability of a bird striking a test object to be $k(t+m)/D$ where k is the number of test obstacles of diameter t stretched across a passage with a width D. The width of the missile or wingspan of the swiftlet is m. The number of obstacle strikes (S) compared to the total number of flights (N) should be approximately equal to $k(t+m)/D$ if the bird is flying at random. Thus the ratio (R) of $k(t+m)/D$ over S/N can be used to indicate the degree of randomness of the swiftlet's flight performance. An R value equal or close to 1 indicates random flight independent of the obstacles, and a value appreciably greater than 1 indicates avoidance behavior. An R value below 1 would indicate deliberate collisions with the obstacles or at least a collision rate greater than predicted by random flight. As also noted by Smyth and Roberts (1983) "this method of analysis is independent of the distance between obstacles, or between an obstacle and the side wall, providing such distance is greater than m." In our calculations a wing span (m) of 28.5 cms was used which is slightly less than the maximum (stretched) wing span (30.16 cm +0.73 SD; Collins unpublished) but more closely approximates the normal wing span of this swiftlet in flight.

Results

The duration of each observation period varied according to the number of birds passing the test apparatus. Thus we have chosen to present data on passes, hits or turns as percentages of the total number of birds observed during each of the observation periods. Before analysis of variance was conducted, the data were arcsine transformed (Sokal and Rohlf 1981). These data were then tested for normality by Lilliefors test and homogeneity of group variance by Box's small sample F approximation for cell counts less than 10; both were not significant (SYSTAT 1990) indicating parametric statistics are appropriate. Since a T-test of within group trials for each of the three test obstacle sizes indicated no significant difference between the percent hits observed under dim light and infrared light (T=.092, P>.05) these two types of observation data were pooled in the subsequent analyses.

An ANOVA indicated that there were significant differences between the percent hits for each of the three obstacle sizes (F = 13.3, P<0.001). Tukey's HSD multiple comparisons indicated that hits of 3.2 mm obstacles was significantly higher than those for both 6.3 mm and 10 mm obstacles while there was no significant difference between the percent hits of the 6.3 mm and 10 mm obstacles. When performance is analyzed as R values (Table 1, Figure 1) all three obstacle sizes appear to be avoided substantially more often than predicted for random flight, although performance with the smallest obstacles is substantially below that for the other two sizes of obstacles. An ANOVA analysis of the percent successful passes through the apparatus also showed a between group significant difference (F= 8.85, P<0.001). Included in this analysis were 4 control tests in which the number of flights through the apparatus area were counted at a time when the cross rope and test obstacles had been lowered to water level. The percent passes during these control periods were significantly higher than the percent passes for all obstacle tests. However, the control periods should be considered more a measure of the normal rate of swiftlet flight traffic through the test area. Accordingly when compared to the sum of both passes and hits by swiftlets passing through the test apparatus the difference is not significant. Similarly, there was no significant difference between the percent turns without any of the obstacles present and the turns made when all of the test obstacles were in place. This suggests that there was not an appreciable difference in the flight behavior of the swiftlets and the rate at which they passed through the test area either when the test apparatus was in place or when it was not. For turns, this may be due to either the swiftlets having sufficient acoustic acuity and memory to note the presence of an inflatable boat on the water and two bamboo poles leaning against the

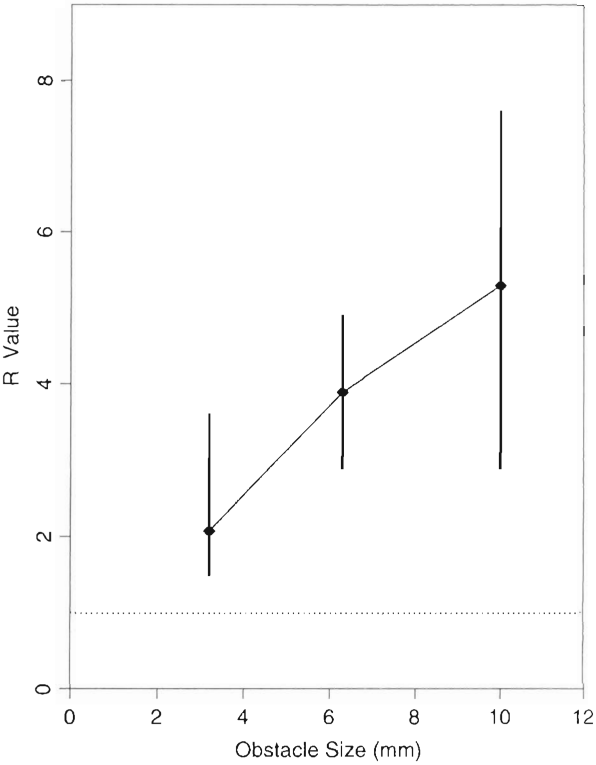


Figure 1. R values for echolocation acuity in Palawan Swiftlets. Random performance (R = 1) indicated by dotted line. Vertical bars indicate range; lines connect means. See text for calculation of R values.

Table 1. Results of echolocation acuity trials with *Aerodramus palawanensis*.

Obstacle Size (mm)	trials (N)	Total observations	Passes (%)	Hits (%)	Turns (%)	R Values mean (SD)
3.2	15	433	29.1	28.9	42.0	2.08 (0.61)
6.3	4	208	31.7	10.6	57.7	3.91 (0.93)
10	7	671	27.9	7.3	64.8	5.33 (1.70)
(Controls)	4	242	58.3	—	41.7	—

walls and reacting accordingly, or the normal maneuvering in the chamber, particularly while approaching nests and roosting sites in the vicinity of the test apparatus. We favor the latter interpretation.

Discussion

A detailed comparison of these data with those presented by earlier workers (Medway 1967, Griffin and Suthers 1970, Fenton 1975, Griffin and Thompson 1982, Smyth and Roberts 1983) is in part confounded by differing methodologies as well as possible interspecific differences. However, the observed differences may be more apparent than real. The electronic technique used by Smyth and Roberts (1983) for detecting obstacle hits for *A. spodiopygius* was more precise than any of the ones used in the other studies. Any contact, including a light brushing by the outer primary feathers of the wing would be scored as a hit. However, Griffin and Suthers (1970) observed that "even in the light [*A. vanikorensis*] avoided obstacles in only about 75% of the trials, probably because gentle touches with the primary feathers caused little discomfort" and that since "the objects were clearly visible, these contacts... must have been due to a failure to dodge the obstacles rather than a lack of sensory information about their location." Field observations of the White-throated Needletail (*Hirundapus caudacutus*) in Australia (Althofer 1937), Vaux's Swift (*Chaetura vauxi*) (Collins 1971) and White-throated Swift (*Aeronautes saxatalis*) (T. Ryan, personal communication) in California confirm that casual contact with naturally occurring environmental obstacles, particularly vegetation, occurs under natural conditions. This may also be a rather routine occurrence in Palawan Swiftlets' natural environment. Thus in experiments of echolocation acuity not all observed hits may indicative of an inability to echolocate the test objects. As noted by Cuthill and Guilford (1990) "successful obstacle avoidance is not simply a function of obstacle perception, but also the accepted collision risk" which can be a graded response and not the all-or-none perhaps implicitly assumed in most studies. Repeated contacts with the abrasive surface of their cave environment could result in an increase in feather wear of swiftlets and a potential impairment of flight. However, none of the swiftlets from the underground river cave examined in this study, all of which had old unmolted outer primaries, showed any pronounced feather wear that could be attributed to this cause (Collins. personal observation). Thus such casual contact would not seem to be particularly detrimental. In the studies of *A. vanikorensis* (Griffin and Suthers 1970), *A. palawanensis* (this study) and *A. spodiopgyius* (Griffin and Thompson 1982) there was some difficulty in analyzing echolocation performance using larger diameter test objects due to the increased inertia of these obstacles and a resultant failure to correctly tally all hits. This was particularly true when this was dependent on visual rather than electronic detection of obstacle movement. In this study, this probably contributed to the elevated performance calculations (higher R values) for swiftlets avoiding the 10 mm test objects as well as the much greater variance in these R values. It is likely that there were also some passes through the test apparatus which involved unobserved minor wing contact with all sixes of test objects and which would have been scored as hits rather than passes by electronic rather than visual methodology. If the rate of observed hits of the test objects in daylight (Griffin and Thompson 1982, Smyth and Roberts 1983) is used as a correction factor (decreasing the percent hits scored electronically) then the data, from the three

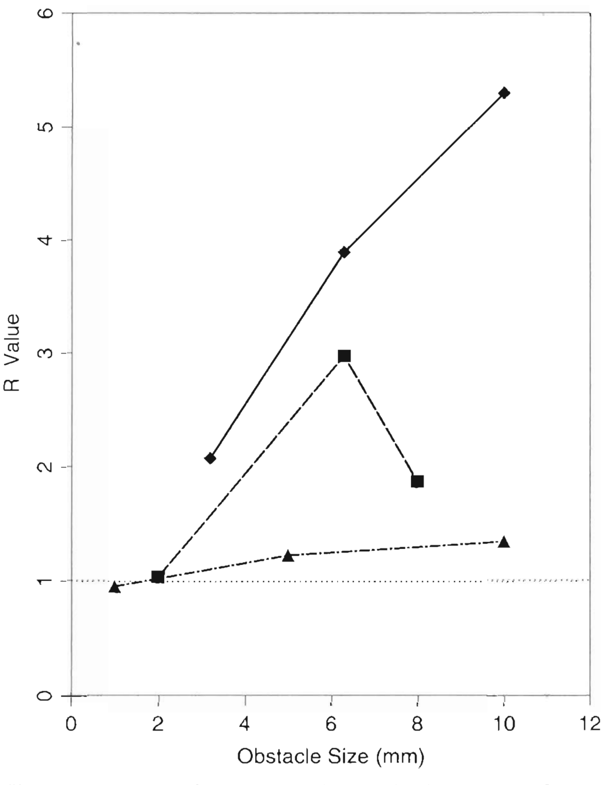


Figure 2. R values for echolocation acuity in three swiftlets: Palawan Swiftlet = solid line (this study); Mossy-nest Swiftlet = dashed line (calculated from Griffin and Suthers 1970); White-rumped Swiftlet = broken line (recalculated from Smyth and Roberts 1983). All lines connect means.

studies from which calculations of R values can be made, show a much greater degree of agreement (Figure 2). In all three studies R values close to 1 (R=0.5 to 1.5), or significantly lower R values than for larger objects, are noted for test obstacles less then 5-6 mm and higher R values for obstacles larger than this. This strongly suggests that the echolocation ability of *Aerodramus* swiftlets shows rather little interspecific variation and that test results from laboratory studies as well as ones done in natural cave settings are in general agreement. This is perhaps to be expected considering the great degree of similarity in the *Aerodramus* swiftlet echolocation signals examined to date (Medway and Pye 1977, Fullard *et al.* 1993). Of particular interest would be acuity studies of the Black-nest Swiftlet (*A. maximus*) which is the only swiftlet so far documented as producing a single rather than double-click echolocation pulse (Medway and Pye 1977). A well developed kinesthetic or spatial memory would seem to be a necessary supplement to the echolocation capacities of swiftlets making daily flights of up to several kms to the back recesses of their nesting caves as well as intricate maneuvers to reach the numerous side chambers utilized in the underground river cave (personal observation). Further investigations of this potentially highly developed sensory capacity in swiftlets would seem appropriate particularly in light of the neurological changes associated with echolocation which have already been documented (Hollander 1974, Cobb 1968).

As pointed out by Smyth and Roberts (1983), despite any remaining differences in the data obtained in the several studies of echolocation acuity of swiftlets, it is clear that it does not begin to match the exceptional capacities of the microchiropteran bats to detect various objects in their environment as well as minute prey items (Simmons *et al.* 1975, Busnel and Fish 1980). Similarly, since the majority of the food items taken by these swiftlets is below the 5-6 mm size of objects which they can locate through echolocation (Harrisson 1971, Smyth 1980, Collins, unpublished) it is extremely unlikely that echolocation plays any role in the food gathering of these diurnal foraging swiftlets. This study supports the previous interpretation that echolocation in *Aerodramus* swiftlets is only used to orient flights within their nesting and roosting caves.

Acknowledgments - We are particularly grateful for permission to conduct these experiments in the St. Paul Subterranean National Park and to Information Officer Ermie V. Aguirre who provided so much help in many ways during our stay. Sincere appreciation is given to The Costeau Society/Équipe Costeau for the economic and logistic support which enabled this research to be conducted. Special thanks to Captain Cousteau for his enthusiastic interest in our efforts to better understand the echolocation abilities of these swiftlets in Palawan. Comments by R. Bray and D. Bradley improved earlier drafts of this paper.

Riassunto - Sono state condotte nelle isole Filippine prove di ecolocazione della Salangana di Palawan (*Aerodramus palawanensis*). La discriminazione di ostacoli con diametro di 3.2 mm e risultata inferiore a ostacoli con diametro rispettivamente di 6.3 e 10 mm. I risultati ottenuti sono in accordo con dati di laboratorio effettuati su altre Salangane e confermano che con ogni probabilita l'ecolocazione è utilizzata nell'orientamento nei siti di riproduzione e riposo, ma non nella ricerca del cibo rappresentato da artropodi di piccola dimensione (<5 mm).

References

Althofer G. W. 1937. Notes on swifts. *Emu* 37:158-159.

Busnell R-G. and Fish J. F. 198C. Animal Sonar systems. *Plenum Publ. Co., New York.*

Cobb S. 1968. On the size of the auditory nuclei in some Apodiformes and Caprimulgiformes. *Auk* 85:132-133

Coleman H. E. 1981. Some observations on swiftlets at the St. Pauls Underground River and environs. pp 86-87 In: (Bruce Mp, ed) The Palawan expedition, Stage II. *Associated Research, Explorations and Aid, Pty. Ltd., Sydney*

Collins C. T. 1971. A probable swift-cactus collision. *Calif. Birds* 2:101.

Cranbrook Earl of and Medway, Lord (1965) Lack of ultrasonic frequencies in the calls of swiftlets. *Ibis* 107:258

Cuthill I. and Guilford T. 1990. Perceived risk and obstacle avoidance in flying birds. *Anim. Behav.* 40:188-190.

Dickinson E. C. 1989. A review of the larger Philippine swiftlets of the genus *Collocalia. Forktail* 4:19-53.

Fenton M. B. 1975. Acuity of echolocation in *Collocalia hirundinacea* (Aves, Apodidae), with comments on the distributions of echolocating swiftlets and molossid bats. *Biotropica* 7:1-7.

Fullard J. H., Barclay R. M. R. and D. W. Thomas. 1993. Echolocation in free-flying Atiu Swiftlets (*Aerodramus sawtelli*). *Biotropica* 25:334-339.

Griffin D. R. 1954. Acoustic orientation in the oil bird, *Steatornis. Proc. Nat. Acad. Sci.* 39:884-893.

Griffin D. R. 1958. Listening in the dark. Yale *University Press, New Haven*

Griffin D. R. and Suthers R. A. (1970) Sensitivity of echolocation in cave swiftlets. *Biol. Bull.* 129:495-501.

Griffin D. R. and Thompson D. 1982. Echolocation by cave swiftlets. *Behav. Ecol. Sociobiol.* 10:119-123.

Harrisson T. 1976. The food of Collocalia swiftlets (Aves: Apodidae) at Niah Great Cave, Borneo. *Jour. Bombay Nat. Hist. Soc.* 71:376-393

Hollander P. 1974. Adaptations for echolocation in cave swiftlets (*Collocalia*). *Unpublished Dissertation, Yale University.* [Dissertation Abst. 34:5746-5747]

Konishi M. and Knudsen E. I. 1979. The oilbird: hearing and echolocation. *Science* 204:425-427

Medway Lord G 1967. The function of echonavigation among swiftlets. *Anim. Behav.* 15:416-420

Medway Lord and Pye J. D. 1977. Echolocation and the systematics of swiftlets. pp 225-238 In: (Stonehouse B. and Perrins C., eds) *Evolutionary ecology*. University Park Press, Baltimore

Novick A. 1959. Acoustic orientation in the cave swiftlet. *Biol. Bull.* 117:497-503

Sibley. C. G. and Monroe B. L. Jr. 1990. Distribution and taxonomy of birds of the world. *Yale Univ. Press, New Haven.*

Simmons J. A., Howell D. S., Suga N. 1975. The information content of bat sonar sound. *Amer. Scientist* 63:204-215

Sokal R. R. and Rohlf F. J. 1981. Biometry. *W. F. Freeman, San Francisco.*

Smyth D. M. 1980. Notes on the diet of the Grey Swiftlet, *Aerodramus spodiopygius*. *Sunbird* 11:20-21

Smyth, D. M. and Roberts J. R. 1983. The sensitivity of echolocation by the Grey Swiftlet *Aerodramus spodiopygius*. *Ibis* 125: 339–345

SYSTAT 1990. SYSTAT 5.0. *Systat Inc., Evanston*

Vincent F. 1963. Acoustic signals for auto-information or echolocation. pp 183-227 In: (Busnel R-G. ed) Acoustic Behavior of Animals. *Elsevier, Amsterdam.*

Avocetta N° 17: 163-175 (1994)

Determinants of clutch size in the tropics; with reference to the White-rumped Swiftlet

MICHAEL K. TARBURTON
3 Freda Court, Blackburn South - Victoria 3130 Australia

Summary – A series of experiments involving clutch and brood-size manipulation, supplemental feeding and nest enlargement were conducted on White-rumped Swiftlets (*Aerodramus spodiopygius chillagoensis*) nesting in savannah habitat in Queensland Australia, so that the birds' reproductive performance might be compared with that of *A.s.assimilis* (Tarburton 1987a) which nests in the tropical rainforests of Fiji. These experiments show that nest-size, predation, synchrony of moult and breeding, and 'competitive release' are each inadequate to explain why the subspecies in the Queensland savannah has a smaller clutch than the subspecies in the rainforests of Fiji. While an inadequate food supply prevents Queensland birds from raising two nestlings at a time it is clear that current interpretations of food limiting theories are inadequate to explain why birds of the Queensland savannah produce a smaller clutch than their conspecifics in rainforests.

Introduction

It has long been established that bird species nesting in the tropical savannah will have larger clutches than the same or closely related species nesting in tropical rainforest (Moreau 1944, Ashmole 1961, Lack and Moreau 1965, Skutch 1967, 1976, Lack 1968, Ricklefs 1970, 1980). While most researchers are agreed that the larger clutch of savannah birds is an adaptive response to a lower population density (Klomp 1970), there is a variety of views as to what controls clutch size.

Lack's theory (particularly as modified by Ashmole 1961, 1963) is widely accepted and probably applies to the tropics more than most theories. This theory proposes that birds achieve maximum reproduction by maximum use of food available to breeding birds. It is suggested that high mortality during the non-breeding season in the savannah, would mean more food per surviving pair in the following breeding season. Having more food than those in a stable environment consequently allows for larger clutches. Skutch (1949, 1967), Cody (1966) and Ricklefs (1980) also reason that high mortality in the non-breeding season would at least be a factor in increasing the clutch size in birds from more seasonal regions of the tropics.

It has been suggested (Winkler and Walters 1983) that studies of exceptions to this widely supported trend should be especially instructive in determining ultimate causes. Because *A. s. chillagoensis* from the savannah environment of Chillagoe, Queensland, Australia, produces a clutch of one, and *A. s. assimilis* from the rainforest environment of Fiji produces a clutch of two, it would appear that this species is an exception to the rule and therefore worthy of study.

Several proximate factors that could be looked at in this species and that have been related to the ultimate determination of clutch size are rainfall, nest-size, predation and competitive release on islands. This paper looks at these proximate factors as they affect this swiftlet's ability to raise nestlings in both regions. Latitude and therefore day length is controlled in this study for both study areas are at the same latitude. As the same species is involved in both studies the chance of interspecific variation is eliminated. The purpose is to help determine what it is that ultimately controls clutch size.

Methods

A sample of nests in Gordale Scar Pot (CH 187) and Guano Pot (CH 146) in the Chillagoe (CH) district of North Queensland was used for controls and for manipulation experiments. Methods used are similar to those used in Fiji (Tarburton 1987a), except that because the only natural clutch is one, it was necessary to manipulate only clutches and broods of two. Only a few single broods were exchanged. Both

Accepted 30 December, 1993

control and manipulated nests were visited six days a week between 28 November 1985 - 27 January 1986 and 2 December 1986 - 23 January 1987. An additional experiment was run simultaneously. It involved enlarging eight nests by gluing a length of 6 mm manila rope along the rim of the nest and to the wall with cyanoacrylic acid ester glue. This made nests as deep, as long and as wide as Fijian nests which normally accommodate two nestlings. In the text all means of measurements are followed by standard errors.

The 1985/6 breeding period is considered a good season with abundant rain and insects while the 1986/7 breeding season is considered to have been a poor season with low rainfall and insufficient food supply. The rain that fell during December and January of the good season represented 152 percent of the average rainfall for this period and this correlated with a much higher density of available insects than was found in the poor season (Tarburton 1994), when for the most part only 35 percent of the average rainfall was recorded. In the dry season very little saliva was used in nest contruction and nests fell apart earlier, possibly contributing to the higher loss of chicks which were slower growing in the dry year. Having a good and a poor season has allowed for a clearer assessment of the birds' ability to feed an extra nestling under both abundant and scarce food supply situations.

Results

Hatching Success

The hatching success of single-egg and two-egg clutches for both the good (1985/86) and the poor (1986/87} seasons at Chillagoe and the comparable results for Fiji are shown in Table 1. The percentage of single-egg clutches hatching in the good season at Chillagoe is not significantly different (Median test, $\chi^2 = 0.24$, n.s.) from the hatching success in the poor season and so the results may be pooled. The pooled average is not significantly different (median test, $\chi^2=0.03$ n.s.) from the hatching rate of single-egg clutches in Fiji. The hatching success of two-egg clutches in the good season at Chillagoe is obviously significantly better than the hatching rate for single egg clutches but was not significantly different (Median test, $\chi^2 = 1.44$, n.s.) from the hatching rate for two-egg clutches in Fiji. Similarly in the poor season at Chillagoe the hatch rate of twin eggs is not significantly different (Median test, $\chi^2 = 1.25$, n.s.) from the hatching rate in the good season and not significantly different (Median test, $\chi^2 = 3.11$, n.s.) from the Fijian hatching rate.

Table 1. Hatching success in the White-rumped Swiftlet.

Sample	Clutch size	Mean ± S.E.	n
Chillagoe 1985/86	1	0.69 ± 0.06	58
Chillagoe 1986/87	1	0.06 ± 0.06	69
Chillagoe both yrs	1	0.64 ± 0.06	127
Fiji	1	0.52 ± 0.09	29
Chillagoe 1985/86	2	1.80 ± 0.09	10
Chillagoe 1986/87	2	0.80 ± 0.40	6
Fiji	2	1.15 ± 0.14	40

Nestling growth

Figures 1 and 2 show the mean daily increase in length of wing and weight for individuals in broods of one and two during the favourable season of 1985/6. The standard errors on the wing growth curves indicate a significant difference between these broods after the eighth day. This divergence occurred earlier than in *assimilis* where it was the tenth day before it was evident that the broods with the extra (third) nestling were dropping significantly behind those in normal sized broods. Average adult wing length was not reached before birds fledged although the minimum adult wing length was reached by most before fledging.

In the poor season of 1986/7 the occurrence of a significant difference between the average wing length of broods of one and two young was delayed until the tenth day (Figure 3). Figure 3 also shows that the wings of nestlings from single broods grew significantly faster in the good year than in the poor year. In all the manipulated two-nestling broods one nestling died and the survivor's wings took an average of 10 days longer than those in one-nestling broods to reach minimum adult length.

The weight of nestlings in broods of two was also significantly lower than the weight of those from single broods. On the fourth day a significant difference could be detected between the weight of those nestlings in single-nestling and two-nestling broods during the good season. The performance in the poor season (Figure 4) was even worse for it was the sixth day before the weight of the single nestlings increased significantly above that of the two-nestling broods. Comparing these measurements with those for *assimilis* nestlings from one and two-nestling broods, which were not significantly different until the 12th day, it is clear that *chillagoensis* is much less able to cope with an extra nestling. Single nestlings reached minimum adult weight by the 17th day whereas

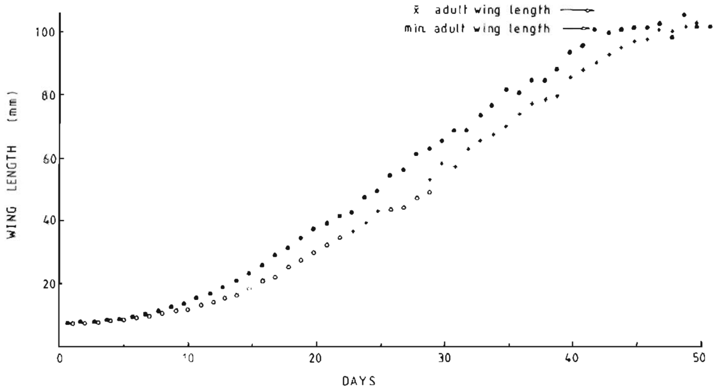


Figure 1. Mean daily increase in wing length of chicks at Chillagoe 1985/6.

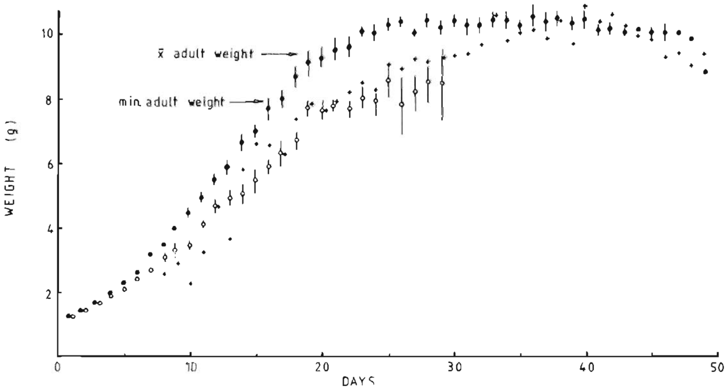


Figure 2. Mean daily increase in weight of chicks at Chillagoe 1985/6.

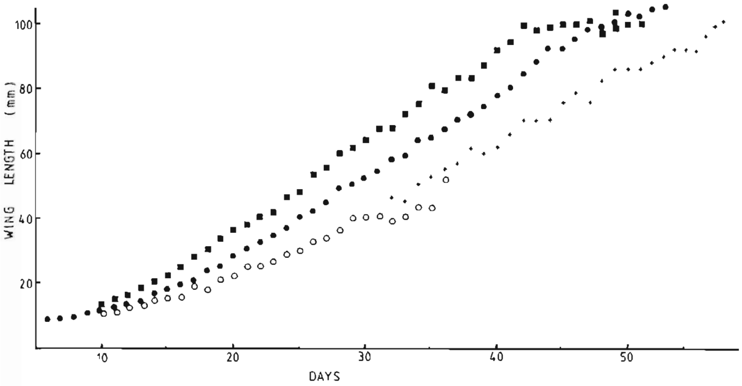


Figure 3. Mean daily increase in wing length of chicks at Chillagoe 1986/7.

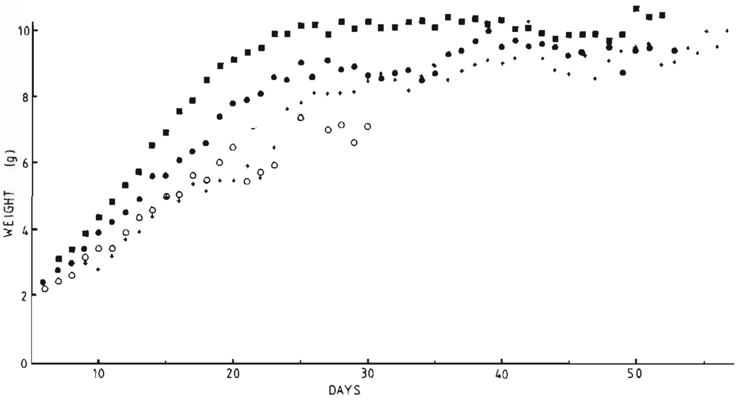


Figure 4. Mean daily increase in weight of chicks at Chillagoe 1986/7.

surviving nestlings from two-nestling broods did not reach adult weight until the 23rd day. These times are respectively only two and one day earlier than those from the same sized broods in Fiji. In the good season, nestlings from single broods did not attain average adult weight until the 36th day. In the poor season it was the 42nd day before the average nestling reached average adult weight.

The long-lasting effect of insufficient food for nestlings in two-nestling broods is shown by the longer time taken by them to reach maximum weight when compared with single-brood nestlings. Another useful measure for making comparisons in nestling growth is the time taken to reach an asymptote (Bradley *et al.* 1984). During the good season single-brood nestlings took 23 days to reach an asymptote whereas the survivors of the two-nestling broods took 35 days to reach the same level. Wing growth in these two-nestling brood survivors was also delayed, taking 47 days to reach 100 mm, whereas single-brood nestlings took only 43 days to reach the same wing length.

By graphing the average daily weight changes in all nestlings per calendar day it became apparent that at periodic intervals the average weight gain was noticeably higher than usual. These days of marked weight increase are shown (Figure 5) to correspond with the first days on which rain fell.

Fledging success

The fledging success for the different sized broods is shown in Table 2. In the good season, *chillagoensis* parents with a brood of two did not raise significantly (Median test, $\chi^2 = 0.02$, n.s.) more nestlings than those with broods of one. The fledging success of single broods was also not significantly different (Median test, $\chi^2 = 0.02$, n.s.) from that raised from single broods in Fiji.

However, in not one case in either the poor or good year at Chillagoe were both nestlings from a two-nestling brood successfully fledged. In the poor season *chillagoensis* with broods of one raised significantly fewer (Median test, $\chi^2 = 5.97$, $P<0.02$) than those raised from single-nestling broods in the good season. In the poor season *chillagoensis* with two-nestling broods raised significantly more (Median test, $\chi^2 = 3.92$, $P< 0.05$) than those raised from single nestling broods in the same season.

Only one nestling fledged from each of the two-nestling broods (n = 8) that were provided with enlarged nests.

Because average growth curves conceal certain characteristics of the individual growth curve and in particular the daily variation within a brood, the daily increase in weight of a selection of individuals has been plotted in Figure 6. The individual growth curves of nestlings from single-nestling broods (Fig. 6b) show greater deviation in response to rain than the deviations for nestlings from two-nestling broods (Fig, 6c) when compared to the average growth curve (Fig. 6a). However, the decline in the weight of nestlings dying by starvation is very clear in the individual growth curves for nestlings from two-nestling broods Fig. 6c). Some nestlings that died did not show weight declines because they fell, or were pushed from their nests while still in good health.

Nest size

One hundred *chillagoensis* nests from Gordale Scar Pot and Guano Pot had an average size of 49.9 ± 0.49 x 42.7± 0.47 x 11.9± 0.42 mm and a volume index of 25.4 cm^3. Thirty-six nests from Fiji averaged 50.0±0.7 x 49.7 ±0.7 x 21.1± 1.0 with an average volume index of 52.4 cm^3.

Feeding rate

By observing a sample of natural and manipulated broods at Chillagoe for one whole day in each season, the data shown in Table 3 were obtained. In the good season the average number of feeding visits per day, to nests with two nestlings was not significantly greater (Median test, $\chi^2 = 0.67$, n.s.) than the number of visits to nests with broods of one. In the poor season it was similarly demonstrated that the average

Table 2. Fledging success in the White-rumped Swiftlet.

Sample	Brood size	Mean ± S.E.	n
Chillagoe 1985/86	1	0.69 ± 0.06	25
Chillagoe 1985/86	2	0.56 ± 0.18	16
Fiji	1	0.43 ± 0.11	27
Chillagoe 1986/87	1	0.31 ± 0.12	12
Chillagoe 1986/87	2	0.71 ± 0.11	11

Table 3. Feeding rate (average number of visits per brood per day) in the White-rumped Swiftlet.

Sample	Brood size	Mean ± S.E.	n
Chillagoe 1985/86	2	4.7 ± 0.67	3
Chillagoe 1985/86	1	5.2 ± 0.30	20
Fiji	1	2.8 ± 0.30	20
Chillagoe 1986/87	1	2.7 ± 0.30	3
Chillagoe 1986/87	2	3.0 ± 0.70	6

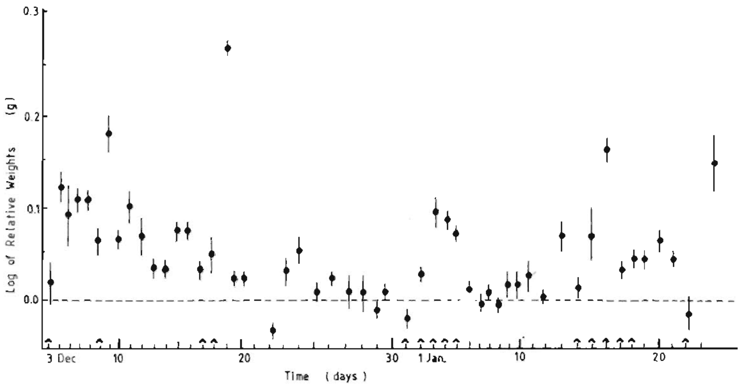


Figure 5. Average daily change in relative chick weights (3 Dec. 1986 - 23 Jan. 1987).

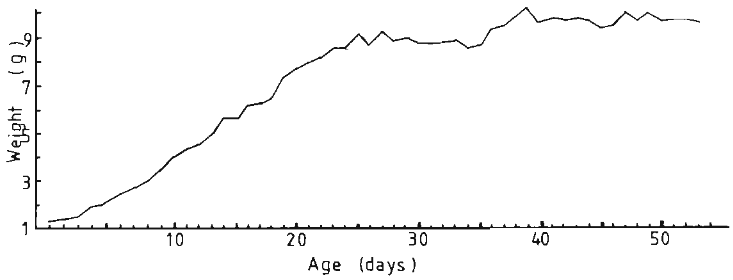


Figure 6a. Average weight increase (1986/87).

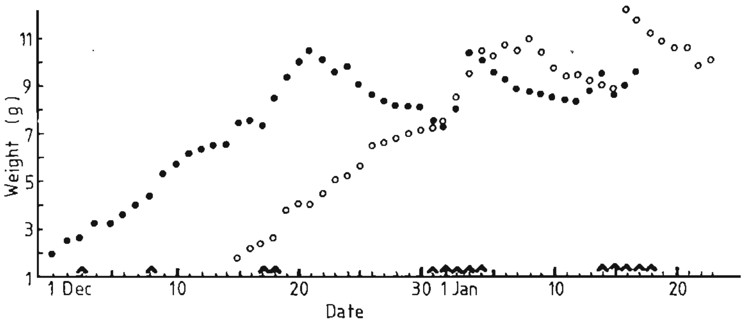


Figure 6b. Daily weight change in two single brood chicks.

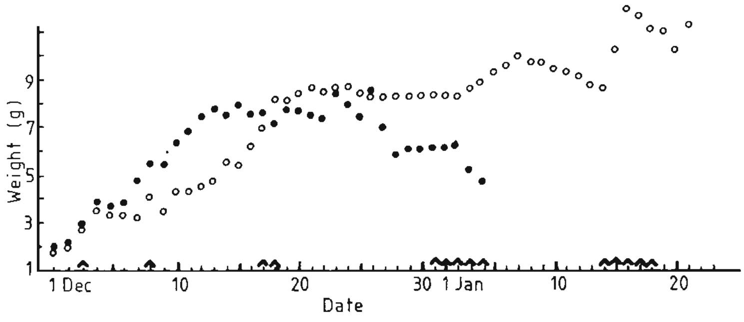


Figure 6c. Daily weight change in a pair of manipulated chicks

number of visits to nests with two nestlings was not significantly greater (Median test, X^2=0.39, n.s.) than the number of visits to nests with one nestling. However, the number of visits to broods of one in the poor season was significantly (Median test, X^2 = 4.2, P< 0.05) fewer than during the good season. The number of visits to two-nestling broods in the poor season was not significantly (Median test, X^2 =0.5, n.s.) less than in the good season. The number of visits to single broods of *chillagoensis* in the good season was significantly greater (Median test, $\chi^2=6.1$, $P< 0.05$) than that of feeding visits to single broods of *assimilis*. In the poor season, however, the number of visits to single broods of *chillagoensis* was not significantly greater (Median test, $\chi^2 = 0.02$, n.s.) than the number of feeding visits to single broods of *assimilis*.

Available food supply

The average number of insects (95± 29) (x ± s.e.) caught in the sweep net samples of available prey in Fiji was significantly more ($t_{32} = 3.0$, $P< 0.01$) than the average number caught in the sweep net during the good year at Chillagoe (9.7 ± 1.0). The average number of insects (5.0 ± 1.1) caught in the sweep net at Chillagoe in the poor year was significantly less ($t_{10}=2.1$, $e < 0.05$) than that caught there in the good year.

Catching more than the average number of insects in the sweep net was significantly (Median test,$\chi^2 = 6.55$, $P< 0.02$) more likely than not, when either, rain fell, or the irrigation sprinklers on the block adjacent to the main sample site had been running in the previous 24 hours. It was also significantly (Median test, $\chi^2=6.55$, $P< 0.02$) more likely that swiftlets would be feeding in the vicinity of the sweep net site on those occasions when the net gathered more than the average number of insects. There was no significant relationship ($\chi^2=2.3$, n.s.) between whether swiftlets were feeding in the area sampled with the sweep net and whether or not rain had fallen (or the irrigation sprinklers used), in the previous 24 hours.

Discussion

In comparing the Whithe-rumped Swiftlets of Fiji and Chillagoe (Queensland), several factors that have complicated other studies on clutch size are avoided. The variation in day length (due to a change in latitude) and hence the unequal time to gather food for breeding puposes is avoided. Problems arising from the observation that some savannah birds are seed eaters, while their rainforest relatives are insect eaters (Lack and Moreau 1965), are also avoided. In fact very few studies comparing clutch size in savannah and rainforest have used the same species.

Despite one season at Chillagoe and two in Fiji which were apparently favourable for gathering food, neither *chillagoensis* nor *assimilis* (Tarburton 1987a) were able to raise significantly more nestlings from artificially enlarged broods than from normal sized broods. These results mean that *chillagoensis* is not responding to the harsh extremes of the savannah climate in the way that a number of theories predict. Rather than producing a larger clutch than *assimilis*, *chillagoensis* produces a smaller clutch. Even the higher fledging rate of two-nestling broods in the poor season at Chillagoe can be explained by the supplementary feeding given to most twins, but not to nestlings in single-nestling broods. This situation therefore needs to be evaluated from several theoretical standpoints.

Clutch size and 'competitive release' on islands

It is commonly stated that island species of birds have smaller clutches than their closest mainland relatives. Lack (1954) gives evidence of this for the limicoline birds from the Falkland islands compared with South America and for ducks (Lack 1968) on a number of remote islands. Cody (1966) cites evidence for smaller clutches in passerines on small oceanic islands off the coast of New Zealand. These examples are all from temperate regions, and when Klomp (1970) includes the Caribbean examples given by Cody (1966) as further examples of reduced clutches on islands, he has missed the point Cody was making. Cody (1966) was predicting, from his model relating clutch size to the birds' allocation of time and energy, that although temperate islands should have reduced clutch sizes, tropical island clutch sizes, if different at all, will be only slight and not necessarily smaller. Cody (1966, 1971) believes birds on temperate islands will have smaller dutches because they are likely to have fewer predators, a more equable climate and larger ecological niches than on the mainland. His reason for predicting little difference between island and mainland clutches in the tropics is that on tropical islands there is little difference in climatic stability and the main deciding factor will be the level of predation on the island. All of these hypotheses assume that the founding individuals were not already genetically constrained to producing one egg at some locations.

On the other hand, Murphy (1968) asserts that predation has nothing to do with clutch size in the tropics and that smaller clutches have evolved on tropical islands in response to the uncertainty of survival from zygote to maturity resulting from populations at or near saturation.

The 100% increase in clutch size that *assimilis* has over *chillagoensis* is not insignificant and therefore is not supportive of Cody's prediction. This is not the only example in the Apodidae where island subspecies have larger clutches than their mainland counterparts. The African Palm Swift has a clutch of two throughout its range on the African continent but a clutch of three on Madagascar (Moreau 1941, Brooke 1971a). That this palm swift also has a more restricted breeding season on Madagascar (Rand 1936) than it does on the mainland, suggests that for islands there is yet to be a full accounting of factors controlling breeding strategies such as clutch size. Other evidence for additional factors is found in the variation in clutch size within a swiftlet species that is found only on the oceanic islands of Micronesia. The Caroline Swiftlet (*Aerodramus inquieta*) lays one egg on Kusaie and Ponape, yet two eggs on Truk Island (Brandt 1966). All three islands are in similar latitudes, have similar altitudes and area, and are similar distances from the Asian mainland.

Two other factors thought to contribute to the regulation of clutch size are predation and nest size *per se*. Both deserve a closer look as data are available for six subspecies of the White-rumped Swiftlet and three subspecies of the Caroline Swifllet to test whether these are factors for regulating clutch size.

The theory that nest size influences clutch size

Quite separate from the effect that food abundance may have on clutch size is the constraint of the nest itself. Snow (1978) has made the point that the structure and the size of the nest has never been properly considered as a factor that limits the maximum clutch-size of a species. He begins by taking the extreme example of the nest of the Tree Swifts (Hemiprocnidae), which can hold only one egg. He suggests that these nests point to a problematic situation rather common in tropical birds: the need for an inconspicuous and inaccessible nest.

However, this cannot apply to the White-rumped Swiftlet which nests in the totally dark sections of caves, making the nests invisible to predators and competitors alike. Inaccessibility is achieved by the placement of the nests on the rock walls and ceilings of the caves, mostly in complete darkness. Such sites offer no restriction as there are considerable areas suitable for nesting in each of the six caves examined in Fiji and at 21 of the 22 caves examined at Chillagoe. These vacant nest sites are not confined to the entrance areas where predation (by Barn Owls (*Tyto alba*) in Fiji, and raptors and cats in Queensland) occasionally occurs, but between areas used for nesting. These areas have roosting bats in them infrequently and predation of birds or bats by the Ghost Bat is rare at Chillagoe.

That some of the swiftlet nests and their nestlings in Guano Pot, Chillagoe, were washed off the wall by seepage from heavy rains in January 1986 suggests another reason why nests may not be built in what appear to be suitable areas of a cave. This also suggests that nest size may be affected by water. Nests becoming wet from water flowing over rock surfaces is apparently more common in the smaller coastal Queensland colonies, where Smyth *et al.* (1980) suggest that this wetting has contributed to the failure of such vulnerable sites in wet years. While it is theoretically possible that building smaller nests would reduce the chance of the nest being on a wet portion of a cave wall, this suggestion has not been researched. The suggestion may benefit from further study as none of the five caves I visited in Fiji, where the birds raise two nestlings, were seen to lose nests due to wetting and so such a pressure to reduce nest size may not exist there. That a number of Apodidae frequently nest behind waterfalls with at least one species regularly building in the spray of waterfalls without detriment to their breeding effort (Stresemann 1928, Somadikarta 1968, Becking 1971) does not necessarily mean that this species can do likewise. However, the second season at Chillagoe was very dry and a number of nests fell apart as a consequence, so both extremes of wet and dry can be detrimental to nest durability .

The common need for the total brood to be effectively warmed by one parent until their feathers grow may place an upper limit on brood size. However, this is not a serious restriction to the Apodidae as the young are resistant to long periods of cooling and as in all swiftlet species the White-rumped Swiftlet is confined to the tropics where cooling is less likely to cause death than in temperate regions. Even in Blue Tits (*Parus caeruleus*) and House Sparrows (*Passer domesticus*) the saving in metabolic energy made by individuals in broods larger than average when the environment was at 15°C was not made at 20°C (O'Connor 1975). As *assimilis* and *chillagoensis* nestlings experience temperatures between 23°C - 26°C it appears that larger broods will not benefit significantly from losing less heat than smaller broods.

It may be suggested that the weight of an extra nestling causes a significant increase in the number of nests that fall from the roof, but none of the nests in Fiji or Chillagoe that were given an extra nestling fell.

Notwithstanding that there is no apparent environmental selection pressure that would favour swiftlets with smaller nests, there is evidence that such pressures exist for other birds. For example the hole-nesting tits lay larger clutches and raise larger broods when given larger nest cavities or larger nest boxes. Ludescher (1973) has shown this in the Marsh Tit (*Parus palustris*) and Willow Tit (*P. montanus*), while Lohrl (1973) demonstrated it in the Great Tit (*P. major*).

In a situation more applicable to the Swiftlets, the

Barn Swallow (*Hirundo rustica*) has been shown to lay significantly larger clutches in larger nests (Møller 1982). So we may well ask does the size of the nest vary in the White-rumped Swiftlet?

The smallest nests measured so far are thirty nests from the Tully Falls Cave in coastal Queensland (Pecotich 1974). These were built by *A.s. terraereginae* and averaged 56 x 45.5 mm in length and width and 3 mm in depth, giving a volume index of 7.6 cm^3. The next largest are the nests of *chillagoensis* with the largest of all being the nests from Fiji. The measurements show that the nests of *assimilis* attain a much larger volume through being much deeper than the nests of either *terraereginae* or *chillagoensis*. From this difference Moller (1982) would correctly predict that the Fijian birds would be the ones to produce the larger clutch. Why then should the Fijian birds produce the larger nests, which Moller suggests leads the laying female to respond by producing a larger clutch?

The answer may depend on the length and therefore the darkness of the caves. The three 'caves' with swiftlets at Tully Falls are very short (the longest is 21m), forcing the birds to nest close to the entrance (Pecotich 1974). It is therefore possible that predatory pressures would exceed those of the Fijian situation where the nests closest to a cave entrance are at least 30m from it. It is possible that greater predatory pressures on *terraereginae* have led to a reduction in nest size and therefore a reduction in clutch size. However, if predation (aided by twilight) was such a selective force how could it explain a clutch of one in *chillagoensis* where all but one of the 27 colonies I visited were in total darkness?

The theory that relates clutch size to predation

Following an experimental increase in brood size that showed predation to be a greater cause for death than starvation, Lill (1975) has suggested that nest predation (selecting for small and inconspicuous nests) rather than the ability of the female to feed the young, has been the main factor determining the natural clutch size of the White-bearded Manakin (*Manacus manacus*). Could it be that predation has directly reduced the clutch size of the two Queensland subspecies of the White-rumped Swiftlet?

Predation may be a stronger force in coastal Queensland, where 'caves' are shorter and therefore the nest sites are better lit, allowing predators to see the colony. There are more species of predators in Australia and so there is a greater chance that at least one is able to utilize swiftlet nest sites.

As the largest Queensland colonies only have 500 nests (Smyth *et al.* 1980), compared with the average of 2,785 nests for five Fijian caves (Tarburton 1987b), it might be that predatory pressure is responsible for the small colony size in Queensland. However, there are many more species of prey in Queensland than in Fiji and the whole concept may not be transferable from manakins to swiftlets as the former are not colonial whereas swiftlets are. Colonial nesting is usually thought of as reducing the effects of predation, at least at the individual level. My discovery of seven new colonies at Chillagoe, including one (Tarby's Swiftlet Pot, CH 379) only 34 m from the previously largest Chillagoe colony (Gordale Scar Pot, CH 187) and four found by other caving club members, brings the number of Chillagoe colonies that were active during the time of this study to 34. This number of colonies and there are surely more is greater than is known for any simaarly sized area of Fiji and so what is lost in colony size by *chillagoensis* is at least partly made up for in the greater number of colonies. So then the smaller colony size at Chillagoe does not necessarily indicate higher predation than in Fiji.

However, higher predatory pressure might exist in coastal Queensland, caused by a lack of long caves suitable for nesting in the dark. The consequent increase in predation when compared with that in Fiji might have reduced nest and brood size making the nest as inconspicuous as possible and the nestling period as short as possible.

Contrary to this proposal is the theoretical consideration given by Perrins (1977). He suggests that birds laying very small clutches and/or having very long incubation periods (White-rumped Swiftlets would be covered by both criteria) will be unlikely to have evolved a reduction in clutch size solely as a result of predatory pressure because the increased risk involved in laying an extra egg would be small (5% in examples used by Perrins, probably 15% in the White-rumped Swiftlet, which does not lay on consecutive days) compared with doubling the number of young raised.

The predation proposal looks less likely when one considers how little the reduction of the height of the nest cup would contribute to hiding a nest from a predator. Recent measurements in Queensland caves have shown that nest sizes vary even within a single cave (Pecotich pers. comm.). This could mean that the published data may not give a true picture of nest size in Queensland: the greater exposure of *terraereginae* nests to sunlight and so possibly to predation remains real. The Caroline Swiftlet (*A.inquieta*) has one subspecies (*A.i.rukenis*) that lays a clutch of two in deep, completely dark caves, and two subspecies (*A. i. inquieta*) and (*A.i.ponapensis*) that lay single-egg clutches in less dark situations (Brandt 1966). An interesting aspect is that the subspecies with the larger clutch is more often found nesting singly or in small groups as well as in large colonies. As solitary nesters are generally more prone to predation, the finding of the dark-nesting subspecies in solitary situations may indicate that nesting in the dark section of caves reduces predation to a very low level. One untested possibility is that the Queensland nests that are in total darkness may be larger (within the limits imposed by the materials available to build them) than those in the twilight, but if this is so why do they not have two eggs?

The theory that predation pressure can influence the size of the clutch (Snow 1978) would suggest that White-rumped Swiftlets nesting in the total darkness of a cave will suffer less predation than those nesting near the entrance or under overhanging rock. If predation had caused the White-rumped Swiftlet to alter its clutch size we would expect those subspecies that use dark caves to be consistent in producing a larger clutch than those nesting in lighted locations. This, however, is not the case. *A. s. terraereginae* generally nests in lighted locations (Pecotich 1982, Smyth *et al.* 1980), while *chillagoensis* pers. obs. and the Samoan subspecies *spodiopygius* (Whitmee 1875), which nest in dark caves, each produce a single-egg clutch. The other subspecies produce two-egg clutches and do so regardless of whether the nests are concealed by darkness or not. On Bougainville Island *A. s. reichenowi* has been found nesting in abandoned mine shafts and under a dead leaning tree (Haddon 1981). In Tonga, *A. s. townsendi* produces its two-egg clutches in sea caves where some nests are only 3 m from the entrance (M. Potts pers. comm.). In New Caledonia *A. s. leucopygia* also appears to nest in twilight situations (Hannecart and Letocart 1980).

A multiple clutch strategy

One means that both Queensland subspecies may use to overcome the restrictions of a smaller clutch than that of the Fijian birds is to produce more than one clutch, apart from replacements. This suggestion is not new; Banfield (1912) suggested that the swiftlets on Dunk Island may rear four clutches in a breeding season and Smyth *et al.* (1980) give some credence to the suggestion, adding that Dunk Island swiftlets have been found breeding from July to April. However, they found only four eggs in July and only one in April, compared with several hundred found in October, November and December, the three months that are clearly the peak laying and incubation period.

On average, a pair of *chillagoensis* take 27 days to incubate their eggs and 47 days to fledge their nestlings. Thus it takes a pair of Queensland swiftlets two and a half months to raise a single brood. To raise the four broods suggested by Banfield would take 10 months without any time for building a nest. However, the summary (Smyth *et al* 1980) of Queensland breeding data (which included the colony Banfield wrote about) in no way indicates that the colony is in peak breeding activity for that long. In fact the Queensland breeding season is no longer than the Fiji season and the activity of early layers, the production of late replacement clutches and annual variation in the commencement and termination dates would better explain the extended, though light, tail-end portion of the breeding period seen in the Queensland data.

Three other factors rule against Queensland birds breeding for ten months. Firstly, the large seasonal variation in rainfall would indicate a large variation in the abundance of aerial insect prey which would not therefore be likely to support breeding for so long if food is the limiting factor in determining clutch size. Secondly, if predation is the mechanism that holds the clutch size to one, surely breeding for ten months would make the parents more vulnerable than when raising as many in half the time. Thirdly, the smaller size of the Queensland colonies tends to indicate that they are not producing twice as many replacements as the Fiji birds, as these birds are almost totally restricted to breeding in their natal colony (Tarburton 1987b).

Regulation of clutch size by stability of food supply

The generalized assumption that where a population and the environment are reasonably stable the clutch size will be at an optimum, has been extended by Hogstedt (1981). He found that the quality (largely determined by food quality and quantity of the territory held by the Magpie (*Pica pica*) determined both clutch size and adult survival. He further suggested that territory quality probably explains the finding that in many passerines the most productive clutch size is larger than that which is most common (Klomp 1970).

In the Apodidae the quality of the territory is correlated with the abundance of flying arthropods, which is correlated with rainfall (Lack 1956, Hespenheide 1975, Emlen 1982). This, in conjunction with Ricklefs' (1980) modification of Lack's hypothesis (that clutch-size is related directly to the resources available during the breeding season and inversely to the density of the population), suggests that there should be a correlation between the evenness of the year's rainfall and clutch-size. To test this I have expressed the average rainfall of the month with the lowest rainfall during the non-breeding season as a percentage of that for the month with the highest rainfall during the breeding season, for several localities where the clutch size for the White-rumped Swiftlet is known.

By following this procedure the resulting figure should be comparable between tropical localities. The data from Koronivia (near the Nasinu Caves in Fiji) gives 39% while those from Tully and Chillagoe (which are near the main breeding caves of the two Australian subspecies) give 13% and 2% respectively. It may be argued that the total rainfall for the year will be more important than the variance between the wet and dry season. However, total rainfall seems less important than the seasonal variation, for, while the Tully district has a higher annual rainfall than Koronivia, Chillagoe's is much lower yet both Australian subspecies produce a clutch of one.

Rainfall data from both the dry and wet sides of New Caledonia indicate low variance (39% and 24% respectively), which is consistent with the fact that on this island this species produces a clutch of two (Hannecart and Letocart 1980). Rainfall for seven Samoan stations (excluding those on the wet south-east margin), averaged 14%. This high variance is consistent with the clutch size of one on these islands (Whitmee 1875). These data indicate that the margin between high and low variance is between 14% and 24%.

Savannah is not the only example of a harsh climate (one having extremes). For example, it has been suggested (Salomonsen 1972) that because Arctic birds sometimes do not breed at all in inclement years, laying a small clutch would be a compromise between breeding and not breeding. In short, it would be expected that Arctic birds would have smaller clutches than temperate birds. Evidence for this reversal of general predictions comes from a study on 15 passerine species (Jarvinen 1986) that breed in southern Finland as well as at a mountain site in Arctic Lapland. Only one of the species produced a larger clutch in the more extreme climate. This view had been predicted by Kendeigh's (1976) suggestion that a species devotes about the same amount of energy to reproduction regardless of where it breeds.

The idea of similar energy being put into reproduction regardless of environment contradicts the theory of r- and K-selection (MacArthur and Wilson 1967) when it is applied to the same species. The 'bet-hedging' theory (Murphy 1968, Schaffer 1974) attempts to solve the discrepancy between the r-and K-selection theory and such observations as given above. By pointing out that mortality in unstable savannah environments is higher for juveniles than in stable environments, 'bet-hedgers' will produce smaller clutches and concentrate on raising a higher percentage than they would from a larger clutch.

Greenslade (1983) suggests that invertebrates respond to not only r- and K-selection pressures, but also to adversity or A-selection pressures, which might be found in predictably unfavourable conditions. One of the suggested responses to this third pressure is reduced fecundity.

Another response to K-selection pressures in birds of harsh environments might be to moult flight feathers while breeding during the short favourable period. Payne (1969) suggests that the general pattern of non-overlap between breeding and moulting means that similar demands on the energy requirements of breeding and moulting operate in both the tropic and temperate regions. Moulting while breeding would also tend to reduce clutch size as both activities take up large amounts of energy and nutrients. Such an effect has been suggested for Arctic birds (Haukioja 1971), and it may be that swiftlets have smaller clutches than most swifts because they moult while breeding, whereas swifts breed and moult at separate times. Data in Table 4 confirm these relationships. Swifts commence moult after laying or after the fledging of their nestlings. However, because swifts are larger than swiftlets and their eggs are proportionately smaller than the adult, swifts could be expected to produce larger clutches even with partial overlap of moult and breeding.

That synchronous moult and breeding restricts brood size in this species is unlikely for both *assimilis* and *chillagoensis* moult while breeding. This means that the only remaining variable between the subspecies that is likely to affect clutch size is the food supply. Because daily growth rate varies with food supply, which varies with rainfall (Figure 5) and the rainfall total and pattern for the two regions differ so much, further consideration should be given to that aspect.

Because the average number of insects caught in the sweep net samples of available prey in Fiji was significantly more than the average number caught during the good year at Chillagoe, and because the average number of insects caught in the sweep net at Chillagoe in the poor year was significantly less than that caught there in the good year, it is clear that it is variation in the abundance of food and not an inability on the part of the bird to collect more food that restricts this swiftlet to raising only one nestling even in a good season at Chillagoe.

The significant relationships between the abundance of flying insects and either rainfall or watering by irrigation, and between the greater likelihood of finding feeding swiftlets overhead on those occasions

Table 4. Synchronization of moult and breeding.

Species	Synchronous	Discreet	Moult after laying	Clutch size	Climate	Source
Apus apus		X		2.3	temp.	Lack and Lack 1951
Apus melba		X		3/4	temp.	Lack and Arn 1947
Apus berliozi		X		2.0	temp.	Brooke 1969
Apus acuticaudis		X			temp.	Brooke 1971a
Apus affinis		X		3.0	trop.	Naik *et al.* 1969
Apus myoptilus		X			trop.	Prigogine 1966
Chaetura brachyura		X		3.8	trop.	Collins 1968a
Chaetura chapmani		X		2/3	trop.	Collins 1968b
Chaetura boehmi		X		3.0	trop.	Brooke 1966
Chaetura ussheri		X		4.0	trop.	Brooke 1971a
Chaetura sabini		X		2.5	trop.	Brooke 1971b
Chaetura cineriventris		X			trop.	Snow 1962
Chaetura pelagica		X		4.2	temp.	Zammuto *et al.* 1979
Chaetura vauxi		X		4-6	temp.	Bent 1940
Cypseloides rutilus		X		1.9	trop.	Collins 1968a
Neafrapus cassini	some	some	some		trop.	Brooke 1971a
Aerodramus fuciphagus		X		2.0	trop.	Langham 1980
Aerodramus maximus	X			1.0	trop.	Medway 1962
Aerodramus spodiopygius	X			1/2	trop.	Tarburton 1986

when the sweep net caught more than average numbers of insects, indicate the dependence of this bird's food supply upon the rainfall. Whether swiftlets were feeding overhead was not significantly correlated to whether rain had fallen (or the irrigation sprinklers had been used) in the previous 24 hours. This lack of correlation is probably due to the birds moving to forage in different areas after several days of rain.

It was the generally low level and high variability in food supply rather than an inability of the parents to obtain food that restricted clutch size to one. If the food was available the parents on those islands were able to collect sufficient for two nestlings. When rain ended a dry period even in the poor season, their nestlings gained weight rapidly (up to one third adult weight in one day). In the good season parents fledged their single broods in the same time as did Fijian birds with single broods. However, with the greater variability of food supply in the poor season, parents took significantly (t_{11}= 3.2, P <0.01) longer to fledge single nestlings than they did in the good season.

Conclusion

Most field data and most models concerned with the regulation of clutch size have shown or predicted that clutch size in birds inhabiting regions with climatic extremes will be larger than that of close relatives living in more uniform environments. However, the White-rumped Swiftlet is an exception, for *chillagoensis* is unable in its savannah environment to raise an artificially enlarged brood of two, whereas *assimilis* normally raises two in the more uniform climate of Fijian rainforest.

This paper has shown that a number of theories are unable to explain this phenomenon. Because enlarging nests did not increase the fledging rate, nest size is not effective in controlling clutch size in *chillagoensis*. Because predators cannot reach the nests of *spodiopygius*, the number of nestlings in a nest cannot influence the rate of predation. Because *chillagoensis* is the mainland subspecies and yet has a smaller clutch than *assimilis*, which is the reverse of that predicted by the theory of "competitive release" on islands, that theory cannot explain the smaller clutch size of *chillagoensis*. Finally, *chillagoensis* does not have enough time to compensate for its smaller clutch by raising two consecutive broods in the normal manner. This is due to the shortness of the wet season, which is shown to coincide with an abundance in the food supply (Hespenheide1975). In other words, food is the limiting factor that prevents *chillagoensis* from raising two nestlings at one time. Nevertheless a newly discovered response to the shortness of the period when food is abundant has been evolved by *chillagoensis* to enable it to raise two nestlings within a season. This is examined in Tarburton and Minot (1987). Further evidence that food is the limiting factor restricting the clutch size of *chillagoensis* to one is shown by the following. Broods with an extra nestling had significantly shorter wings than those in natural broods of one by the eighth day, while the average weight of the same nestlings fell significantly behind that of the two-nestling broods earlier than *assimilis* nestlings from artificially enlarged broods. This is taken to indicate the greater difficulty *chillagoensis* has in collecting adequate food for two nestlings.

That *chillagoensis* made significantly fewer feeding visits to nestlings in the poor season than in the good season and that two-nestling broods were not fed significantly more often than single-nestling broods in either the poor or good season, indicates that this bird is struggling to adequately feed one nestling in a poor season and cannot feed two nestlings even in a good season. The correspondence between days of largest weight gain to the first days of each bout of rain further demonstrates the need for frequent rains in the maintainance of high food levels. Together, these data suggest that a lack of available food was the major cause preventing *chillagoensis* from fledging significantly more nestlings from manipulated two-nestling broods than from natural single-nestling broods. So it is the reliability as well as the quantity of food that determines clutch size in the White-rumped Swiftlet in the tropics.

Acknowledgements – I gratefully acknowledge financial assistance for transport from the Frank M.Chapman Memorial Fund of the Americam Museum of Natural History. Dr. Edward 0. Minot helped both in the field and in giving useful advice on drafts of this paper.

I thank the Queensland National Parks and Wildlife staff at Chillagoe (particularly J. Barton, D. Flett, J. Fred, L. Leafe, and L. Little) and the Chillagoe Caving Club (particularly A. Cummins, K. Offer, T. Porritt and K. Ridgway) for help in the field. Thanks are due to the Queensland National Parks and Wildlife Service (ONPAWS), Brisbane, for permission to enter the Chillagoe sites which are within Chillagoe National Park.

Riassunto – In ambiente di savana nel Queensland australiano si sono effettuati esperimenti di manipolazione del numero di uova e di nidiacei, con nutrizione artificiale e ingrandimento del nido di *Aerodramus spodiopygius chillagoensis*.

Le condizioni riproduttive così create sono paragonabili a quelle affrontate dalla sottospecie *A. s. assimilis* che nidifica nelle foreste pluviali di Fiji.

Questi esperimenti hanno dimostrato che la dimensione del nido, la predazione, la sincronia di muta e di nidificazione non sono parametri in grado di spiegare il motivo per cui la sottospecie di savana del Queensland ha una dimensione della covata minore rispetto alla sottospecie di Foresta a Fiji. Anche se carenze di cibo possono impedire alle coppie del Queensland di allevare due nidiacei, occorre notare che le attuali interpretazioni teoriche sulle disponibilità alimentari non possono spiegare covate minori dei loro conspecifici della foresta pluviale.

References

Ashmole N.P. 1961. The biology of certain terns. D.Phil. thesis (Oxford): cited by Lack and Moreau 1965.

Ashmole N.P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103b: 458-473.

Banfield E.J. 1911. My tropical isle. London. Fisher Unwin.

Becking J.H. 1971. The breeding of *Collocalia gigas*. *Ibis* 113: 330-334.

Bent A.C. 1940. Life histories of American Cuckoos, Goatsuckers, Hummingbirds & their alies. *U.S. Nat. Mus. Bull.* 176: 254271 .

Brandt J.H. 1966. Nesting notes on the Collocalia of Micronesia and Peninsular Thailand. *Oologists Rec.* 40: 61-63 .

Brandley D.W., Landry R.E. and Collins C.T. 1984. The use of jackknife confidence intervals with the Richards curve for describing avian growth patterns. *Bull. S. Calif. Acad. Sci.* 83: 133-147

Brooke R.K. 1966. The bat-like spinetail *Chaetura boehmi* Schalow (Aves). *Arnoldia* 2: 1-18.

Brooke R.K. 1969. *Apus berliozi* its races and siblings. *Bull. Brit. Ornith. Club* 81: 11-16.

Brooke R.K. 1971a. Breeding of Swifts in Ethiopian Africa & adjacent islands. *Ostrich* 42: 5-36.

Brooke R.K. 1971b. Taxonomic and distributional notes on the African Chaeturini. *Bull. Brit. Ornith. Club* 91: 76-79 .

Cody M.L. 1966. A general theory of clutch size. *Evolution* 20: 174-184.

Cody M.L. 1971. Ecological aspects of reproduction. Avian Biology (Ed. by D.S. Farner & King, J.R.) pp 461-512. *New York. Academic Press.*

Collins C.T. 1968a. The comparative biology of two species of swifts in Trinidad, West Indies. *Bull. Florida State Mus.* 11: 257-320.

Collins C.T. 1968b. Notes on the biology of Chapman's Swift *Chaetura chapmani* (Aves:Apodidae). *Am. Mus. Novit.* 2320: 1-15.

Emlen S.T. 1982. The evolution of helping. I. An ecological constraints model. *Am. Nat.* 119: 29-39.

Greenslade P.J.M. 1983. Adversity selecbon and the habitat templet. *Am. Nat.* 122: 352-365.

Haddon D. 1981. Birds of the North Solomons. *Wau Ecol. Inst. Wau.*

Hannecart F. and Letocart Y. 1980. Oiseaux de Nouvelle Caledonie et des Loyautes vol.1. *Auckland. Clark and Matheson.*

Haukioja E. 1971. Summer schedule of some subarctic passerine birds with reference to postnuptial moult. *Rep. Kevo Subarctic Res. Stat.* 7: 60-69.

Hespenheide H.A. 1975. Selective predation by two swifts & a swallow in Central America. *Ibis* 117: 82-99 .

Hogstedt G. 1961. Should there be a positive or negative correlation between survival of adults in a bird population and their clutch size? *Am. Nat.* 11B: 568-571.

Jarvinen A. 1986. Clutch size of passerines in harsh environments. *Oikos* 46: 365-371.

Kendeigh S.C. 1976. Latitudinal trends in the metabolic adjustments of the House Sparrow. *Ecology* 57: 509-519.

Klomp H. 1970. The determination of clutch-size in birds. A review. *Ardea* 58: 1-124.

Lack D. 1954. The natural regulation of animal numbers. *Oxford Uni. Press. London.*

Lack D. 1956. Swifts in a tower. *London. Methuen.*

Lack D. 1968. Ecological adaptations for breeding in birds. *London. Methuen.*

Lack D.and Arn H. 1947. Die bedeutung der gelegrobe beim alpensegler. *Orn. Beob.* 44: 188-210.

Lack D.and Lack E. 1951. The breeding biology of the Swift *Apus apus*. *Ibis* 93: 501-546.

Lack D. and Moreau R.E. 1965. Clutch-size in tropical passerine birds of forest savannah. *L'Oiseau* 35: 76-89.

Langham N. 1980. Breeding biology of the Edible-nest Swiftlet *Aerodramus fuciphagus*. *Ibis* 122: 447-460.

Lill A. 1975. The evolution of clutch size and male "chauvinism" in the White-bearded Manakin. *Living Bird* 13: 211-231 .

Lohrl H. 1973. Einflusser brutraumflache auf die gelegegrosse der kohlmeise (*Parus major*). *J. fur Ornithologie* 114: 339-347.

Ludescher F.B. 1973. Sumpfmeise (*Parus palustris palustris L.*) und weidenrneise (*Parus montanus salicarius* Br.) als symatrische zwillingsarten. *J. fur Ornithologie* 114: 3-56.

McArthur R.H. & Wilson E.O. 1967. The theory of island biogeography. *Princeton. Princeton Uni. Press.*

Medway L. 1962. The swiftlets (*Collocalia*) of Niah Cave, Sarawak. 1. Breeding Biology. *Ibis* 104: 45-66.

Møller A.P. 1982. Clutch size in relation to nest size in the swallow (*Hirundo rustica*). *Ibis* 124: 339-343.

Moreau R.E. 1941. A contribution to the breeding biology of the Palm-swift *Cypselus parvus* . *J. E. Afr. and Uganda Nat. Hist. Soc.* 15: 154170.

Moreau R.E. 1944. Clutch size: a comparative study with special reference to African birds. *Ibis* 86: 286-347.

Murphy G.I. 1968. Pattern in life history and the environment. *Am. Nat.* 102: 390-404.

Naik R.M. and Shivanarayan N. 1969. Moult of the primary feathers in the House Swift, *Apus affinis* . *Pavo* 7: 19-42.

O'Connor R.J. 1975. The influence of brood size upon metabolic rate and body temperature in nestling Blue Tits *Parus caeruleus* and House Sparrows *Passer domesticus*. J. *Zool. Lond.* 175: 391-403.

Payne P.B. 1969. Overlap of breeding & moulting schedules in a collection of African birds. *Condor* 71: 140-145.

Pecotich L. 1974. Grey Swiftlets in the Tully River Gorge & Chillagoe Caves. *Sunbird* 5: 16-21.

Pecotich L. 1982. Speciation of the Grey Swiftlet *Aerodramus spodiopygius*. *Tower Karst* 4: 53-67.

Perrins C.M. 1977. The role of predation in the evolution of clutch size. Chapter 16. In: Stonehouse, B. and Perrins, C.M. Edits *Evolutionary Ecology. London. Macmillan.*

Prigogine A. 1966. Note on Chapin's Swift. *Bull. Brit. Ornith. Club.* B6:1-5.

Rand A.L. 1936. The distribution and habits of Madagascar birds. *Bull. Amer. Mus. Nat. Hist.* 72: 143-499.

Ricklefs R.F. 1970. Clutch size in birds: outcome of opposing predator & prey adaptations. *Science* 168: 599-600.

Ricklefs R.F. 1980. Geographic variation in clutch size among passerine birds: Ashmoles hypothesis. *Auk* 97: 38-49 .

Salomonsen F. 1972. Zoogeographical and ecological problems in Arctic birds. *Proc. XV Int. Orn. Congr.*: 25-77.

Schaffer W.M. 1974. Optimal reproductive effort in fluctuating environments. *Am. Nat.* 108: 78-790.

Skutch A.F. 1949. Do tropical birds rear as many young as they can nourish. *Ibis* 91: 430-455.

Skutch A.F. 1967. Adaptive limitation of the reproductive rate of birds. *Ibis* 91: 579-599.

Skutch A.F. 1976. Parent birds and their young. *Texas. Univ. of Texas.*

Smyth D.M., Pecotich L. and Roberts J.R. 1980. Notes on the distribution and breeding of the Grey Swiftlet, (*Aerodramus spodiopygius*). *Sunbird* 11: 1-19.

Snow D.W. 1962. Notes on the biology of some Trinidad Swifts. *Zoologica* 47: 129-139.

Snow D.W. 1978. The nest as a factor determining clutch-size in tropical birds. *J. fur Ornith.* 119: 227-230.

Somadikarta S. 1968. The Giant Swiftlet, (*Collocalia gigas*), Hartert and Burler. *Auk* 85: 549-559.

Stresemann E. 192B. Sauropsida:Aves.In W. Kukenthal (Ed.), Handbuch der Zoologie, 7. Halfte, Lieferung 4. *Berlin: Walter de Gruyter.*

Tarburton M.K. 1986. A comparison of the flight behaviour of the White-rumped Swiftlet and the Welcome Swallow. *Bird Behaviour* 6: 72-34.

Tarburton M.K. 1987a. An experimental manipulation of clutch and brood size of White-rumped Swiftlets *Aerodramus spodiopygius* of Fiji. *Ibis* 129: 107-114.

Tarburton M.K. 1987b. The population status, longevity and mortality of the White-rumped Swiftlet in Fiji. *Corella* 11: 97-110.

Tarburton M.K. and Minot E.O 1987. A novel strategy of reproduction in birds. *Anim. Behav.* 35: 189.

Whitmee S.J. 1875. List of Samoan birds, with notes on their habits & c. *Ibis* 5: 436-447.

Winkler D.W. and Walters J.R. 1983. The determination of clutch size in precocial birds. *Current Ornithology* 1:33-68

Zammuto R.M. and Franks E.C. 1979. Trapping flocks of Chimney Swifts in Illinois. *Bird Banding* 50: 201 - 209.

Avocetta N° 17: 177-188 (1993)

Effets du climat sur la reproduction du Martinet noir (*Apus apus* L.). Synthèse des observations réalisées dans le Sud de la France

GÉRARD GORY

Museum d'Histoire Naturelle, 13bis, boulevard Amiral Courbet - 30000 Nimes, France

Résumé - L'analyse de 13 années d'observations réalisées sur une colonie de Martinet noir (*Apus apus* L.) implantée dans les murs du Museum D'Histoire Naturelle de Nimes (Gard-France), montre que le succès de reproduction de cette espèce est en relation avec les facteurs climatiques. Nous constatons que certaines caractéristiques du climat méditerranéeen (par exemple les vents) qui, en immobilisant probablement l'entomofaune, ralentissent l'accumulation de l'énergie nécessaire à la production d'oeufs, ont un effet sur l'initialisation, la chronologie et la taille des pontes. De même, l'action de ces facteurs en période d'élevage des poussins perturbe l'évolution de leurs courbes pondérales. Si la présence de fortes précipitations reste rare sous ce type de climat au printemps (1 cas en 13 années), nous constatons qu'une varation importante des températures a des conquénces sur la survie des poussins et celle des adultes reproducteurs. Il ressort de notre étude que si certains facteurs météorologique semblent plus importants (température, précipitation), ce sont surtout les vents de secteur nord-nord ouest qui, en agissant de manière plus marquée sur les disponibilités alimentaires, sont les facteurs les plus determinants quant à la réussite de la reproduction du Matinet noir.

Introduction

L'étude de la dynamique d'une population d'oiseaux implique une approche démographique de l'espèce concernée, et une analyse des mécanismes impliqués dans sa régulation numérique, qui dépendent à la fois de la structure de la population et de son environnement écologique (Blondel 1975). Nicholson (1945) et Solomon (1959) ont mis en évidence le rôle des facteurs intrinsèques à la population. Au contraire, Andrewartha & Birch (1954) ont considéré que la variabilité des paramètres écologiques extrinsèques à la population (par ex: climat, nourriture...), était l'agent régulateur et limitant des populations. Lack (1954, 1966), a trouvé une corrélation positive entre la densité instantanée d'une population et l'abondance de sa nourriture bien que selon lui, les facteurs extrinsèques n'interviennent pas de façon décisive dans la régulation des effectifs.

Il peut paraître particulièrement intéressant dans ce contexte théorique, d'étudier une espèce chez qui l'abondance ou la disponibilité de la nourriture dépendent directement du climat. Le climat, surtout lorsqu'il est de type contrasté, peut en effet, jouer sur les disponibilités alimentaires, et agit donc indirectement sur la variation des effectifs (Ribaut 1964, Cody 1971, Thibault *et al.* 1987, Gory 1992). Le cas du Martinet noir (*Apus apus*) semble ici approprié. En effet, Taylor (1963), puis Elkins (1983), ont montré que l'abondance de l'entomofaune était liée à la température de l'air. O' Connor (1979) a mis en évidence une corrélation significative entre la date de la ponte chez le Martinet noir et la température de l'air des trois semaines précédentes, corrélation que Vizyova et Janiga (1986) ont retrouvée lors de la croissance des poussins. Lack et Lack (1951), ont signalé des fluctuations dans la durée d'élevage des poussins, résultant en partie d'une sous-alimentation en période de mauvais temps. Dans les pays méditerranéens, les travaux de Finlayson (1979), Rodriguez de los Santos et Rubio Garcia (1986) en Espagne, ceux de Boano et Cucco (1989), Farina (1980) et Malacarne et Cucco (1991) en Italie, ceux de Gory (1987) et Thibault *et al.* (1987) en France, ont contibué à une meilleure connaissance de la biologie des Apodidae en soulignant bien qu'accessoirement, les effets du climat.

Les caractéristiques du climat méditerranéen (Di Castri 1981, Nahal 1981), nous ont conduits à analyser ses effets sur la reproduction du Martinet noir. Le présent travail se propose de faire la synthèse de 13 années d'observations quotidiennes sur une colonie urbaine implantée dans le Sud de la France (Gory 1988).

Accepted 30 October, 1993

Methodes

Site et rytme d'observation. Cette étude repose sur l'observation de 143 cavités, implantées dans une bâtisse de la fin du XVII siècle, dont 54 ont été aménagées pour permettre une observation directe (Gory 1988). Nous avons assuré une surveillance quotidienne de ces nids de l'arrivée des oiseaux à l'envol des jeunes, complétée par des enregistrements automatisés en continu (Gory et Jeantet 1986). Quatorze nids ont été équipés de détecteurs de chaleur simplifiés,dont le principe est basé sur la porpriété du seuil de conduction directe des diodes à jonction au silicium qui varie suivant une fonction linéaire inverse de la température de la jonction (Gory et Jeantet 1988). Aprés plus de 12.960 heures d'enregistrements, ces appareils nous permettent d'évaluer le temps de présence d'un oiseau sur son nid. Ainsi, quatre nids ont été suivis pendant trois années (1986, 1987 et 1988), ce qui correspond à 1326 heures d'enregistrement analysées. Les courbes de croissance pondérale des poussins ont été réalisées à partir de relevés quotidiens obtenus grâce à une balance de précision (Mettler P 163 N).

Données météorologiques. Les relevés climatologiques ont été obtenus à la station de météorologie nationale de Nimes-Courbessac (altitude 59 m), située à trois kilométres de la colonie. Les données utilisées pour ce travail concernent: la hauteur des précipitations (en mm), la température de l'air sous abri (moyenne des minima + moyenne des maxima /2, en degrés C), la direction et la vitesse du vent vectoriel moyen (en m/s, anémometre placé à 10 m au-dessus du sol).

Caractéristiques du climat méditerranéen. L'irrégularité du climat méditerranéen nous a conduit à distinguer les années qui présentaient des écarts importants par rapport aux moyennes, ce qui nous permettra d'en évaluer les répercutions sur le déroulement de la reproduction.

Précipitations. La Figure 1 présente la hauteur des précipitations mensuelles entre les mois d'avril et d'août, en données cumulées sur 44 ans, et pour les années 1991 et 1992. Nous avons noté que l'année 1991 était déficitaire en pluie (500 mm contre 734 mm pour la période 1946-1990), en revanche l'année 1992, bien que déficitaire pour les mois d'avril et mai, présentait des précipitations excédentaires en juin, juillet et août,.

Températures. L'histogramme de la Figure 2 représente les températures moyennes décadaires relevées pour la période 1945 -1990 comparées aux années 1987 et 1991. On notera que les mois de mai et juin 1987 étaient caractérisés par des périodes froides (températures inférieures à la normale). Le printemps 1991, était frais en moyenne avec des températures clémentes jusqu'au 15 avril puis nettement plus fraîches ensuite.

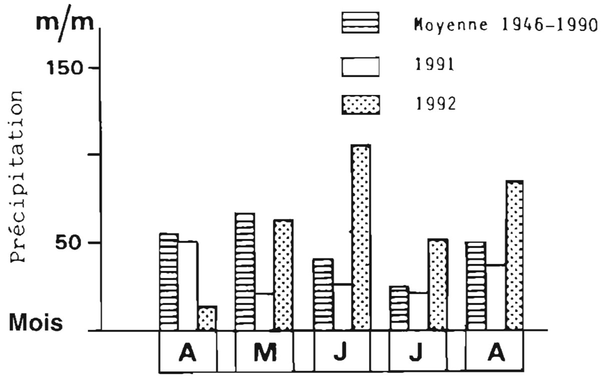


Figure 1. Hauteur des précipitations d'avril à août; 1991 (en blanc), 1992 (grisé) et cumul moyen pour la période 1946 - 1990 (hachure). *Rainfall between april and august: 1991 (white), 1992 (grey) and average for the period 1946-1990 (hatched histograms).*

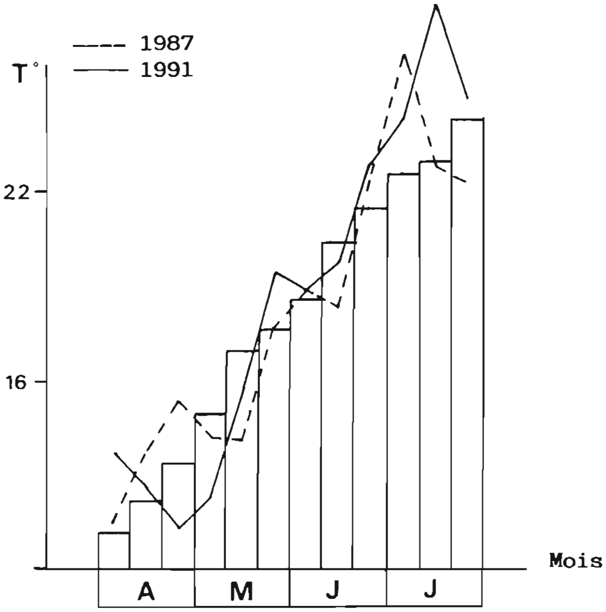


Figure 2. Températures moyennes décadaires d'avril à juillet; 1987 (tirés), 1991 (traits pleins) et cumul moyen pour la période 1945 - 1990 (histogramme). *Mean temperatures (decades) between april and july; 1987 (broken line), 1991 (continuous line) and average for the period 1945-1990 (histogram).*

Tableau 1. Nombre de nids à 1, 2, 3 et 4 oeufs entre 1980 et 1992. *Clutch size of the Common Swift in the study colony between 1980 and 1992.*

NOMBRE D'OEUFS		ANNÉES													PONTES	
		1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	nb	%
	1				1	1		2	1	3	3	2	1	3	17	4,81
Première	2	2	10	6	6	12	13	7	16	20	15	14	22	16	159	45,04
ponte	3	12	9	15	13	8	11	13	10	12	19	19	16	13	170	48,20
	4			1	3	2					1				7	1,98
Ponte de	1									1	1	1		1	4	
remplacement	2				2	1		1	1	1		1	1		8	

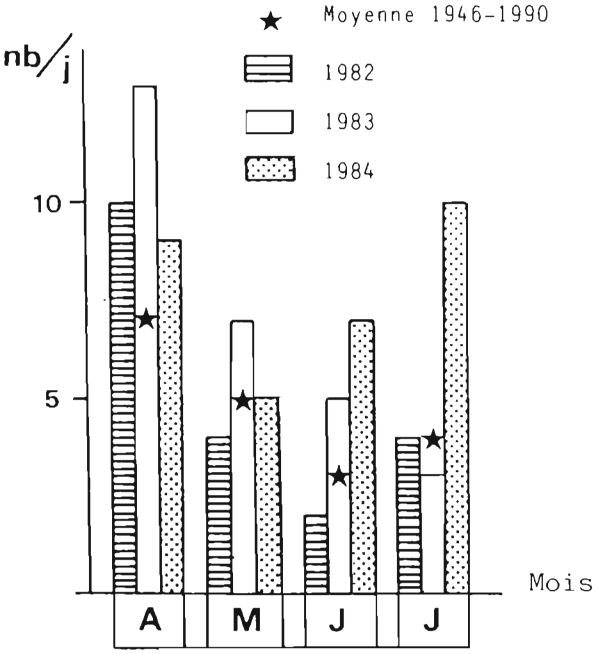


Figure 3. Nombre de jours de vent fort ≥ 16,11 m/s d'avril à juillet; 1982 (hachure), 1983 (en blanc), 1984 (grisé), * = cumul moyen pour la période 1946 - 1990. *Number of days with high wind speed (i.e., ≥ 16,11 m/s, between april and july; 1982 (hatched histograms), 1983 (white) 1984 (grey), * = average for the period 1946-1990.*

Vents. Nous avons comparé le nombre de jours de vent fort ≥ 16,11 m/s pour les années 1982, 1983 et 1984 (vent élevé), 1987 et 1991 (températures fraîches), 1991 (déficit en précipitation) et 1992 (excès en précipitation). Les autre années (1985,1986,1988,1989 et 1990) seront considérées comme normales.

Resultats

Au printemps, les premiers oiseaux étaient présents sur la colonie dans la deuxième décade d'avril (dates extrêmes: 3-28 avril, n = 22 ans). De 1980 à 1988, la chronologie de l'installation au nid a montré que 81% des futurs reproducteurs (n = 346) étaint installés dés la première décade de mai, et que l'initialisation des pontes avait lieu courant mai (dates extrêmes: 6-27 mai, n = 893 oeufs de 1980 à 1992). L'envol des poussins s'échelonnait du 6 juillet au 17 août (n = 546).

La ponte.

Les pontes se sont échelonnées sur une période minimale de 27 jours en 1982 et maximale de 43 jours en 1984. De 1982 à 1992, 51% des oeufs ont été pondus entre les 17 et 31 mai, nous avons noté un décalage de 15 jours entre la date moyenne de pontes des années 1983 et 1991 (Figure 4), ainsi qu'une différence dans la taille des pontes en fonction des années (Tableau 1; G = 22.95; p = 0,028).

Influence des facteurs météorologiques sur le déroulement de la ponte. Pour les six années considérées (Figure 5), on notera qu'en période prépositale seules les années 1983 (13mm sur 2 jours), 1987 (1,1 mm en une journée) et 1991 (20,8mm sur 2 jours) ont présenté des pluies. Pendant la ponte, les précipitations restent faibles (4 à 12 jours), et localisées en fin de ponte (1982, 1987, 1991). Seules les années 1984 (157.1 mm) et 1992 (95.4 mm) ont présenté des précipitations abondantes, bien que dans ce dernier cas, ces pluies aient eu lieu au moment où 88% des oeufs étaient déjà pondus. En climat méditerranéen les précipitations sont très localisées et limitées dans le temps. L'examen de la

Figure 5 suggère que l'effet des précipitations sur le déroulement de la ponte du Martinet noir n'est pas prépondérant. Trois cas de figure apparaissent quant au déroulement des pontes selon les années (Figure 4): étalement de la ponte limité dans le temps (1982, 1991 et 1992), ou au contraire plus long (1984) ou enfin séparé en deux pics (1983 et 1987). Les années 1982 et 1992 se caractérisaient par un pic de pontes rapidement atteint et un faible étalement de la ponte (Figures 4 et 5). Or ces deux années présentaient un mois de mai chaud, et trés sec pour ce qui est de 1982 (le plus sec depuis 1921). En revanche en 1991, l'initialisation de la ponte était repoussée à la fin de la troisième décade de mai, mais restait très contractée (Figures 4 et 5). Mai 1991 était un mois frais, sec et venté. Ainsi aprés deux premières décades froides, la troisième était chaude et correspondait au début de la ponte. Ces différents résultats suggèrent donc que les températures (en mai) aient un rôle dans le déclenchement et le déroulement des pontes chez le Martinet noir. En 1991 ce phénomène était de plus accentué par la présente de vents dominants de secteur nord, le nombre de jours de vent fort constituent, pour un mis de mai, un nouveau record. On notera que la fin de la présence du vent du nord le 27 mai, marque le début de la ponte. Un résultat similaire apparaît en mai 1984, mois marqué par une présence du vent de secteur nord du 8 au 13 (8,4 m/s le 8 mai), avec pour

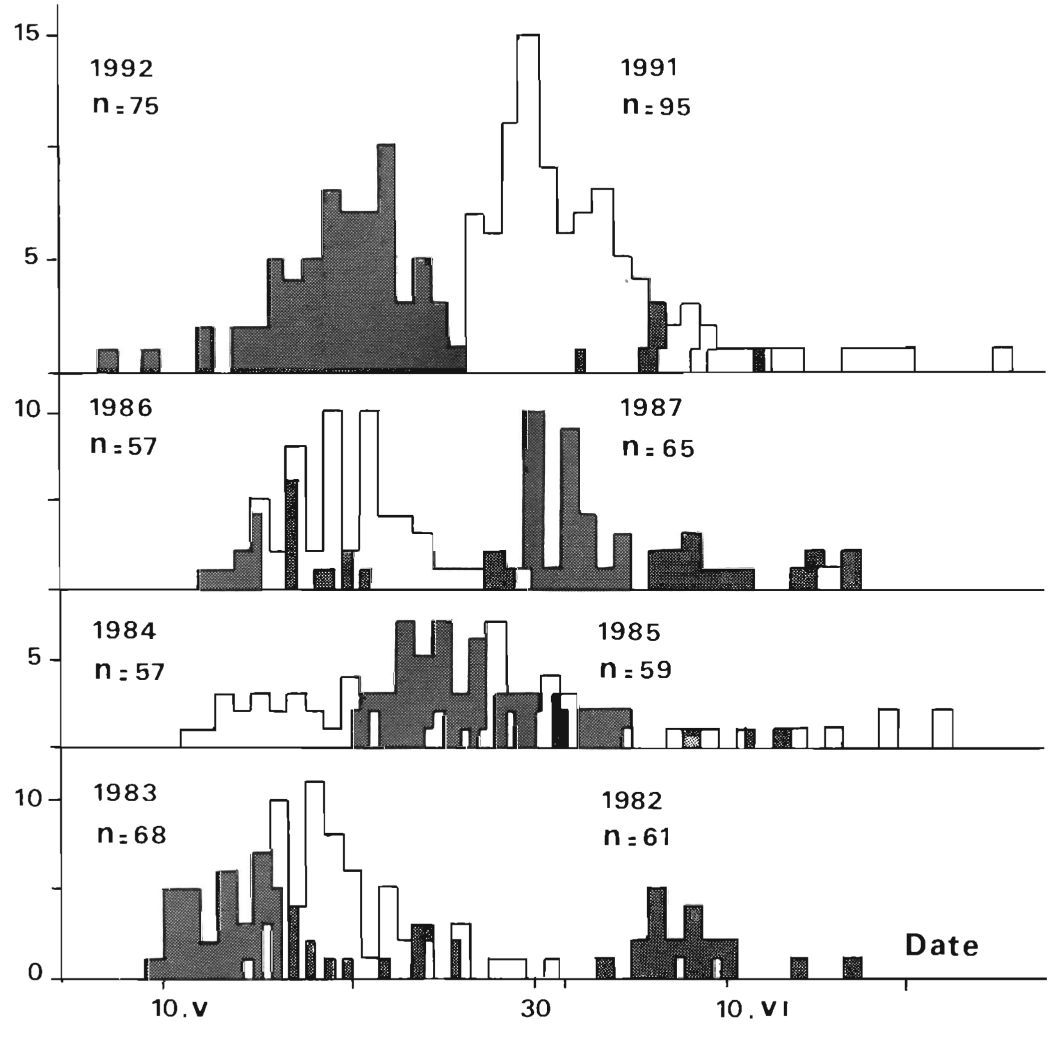


Figure 4. Chronologie des pontes. En blanc: 1982, 1984, 1986 et 1991. En noir: 1983, 1985, 1987 et 1992. n = Nombre d'oeufs pondus par année. L'année 1986 peut être considérée comme une année normale (voir texte). *Timing of laying in the Common Swift at Nîmes. In white: 1982, 1984, 1986 and 1991. In black: 1983, 1985, 1987 and 1992. n = Number of eggs layed each year. 1986 is considered as normal year (see text for details).*

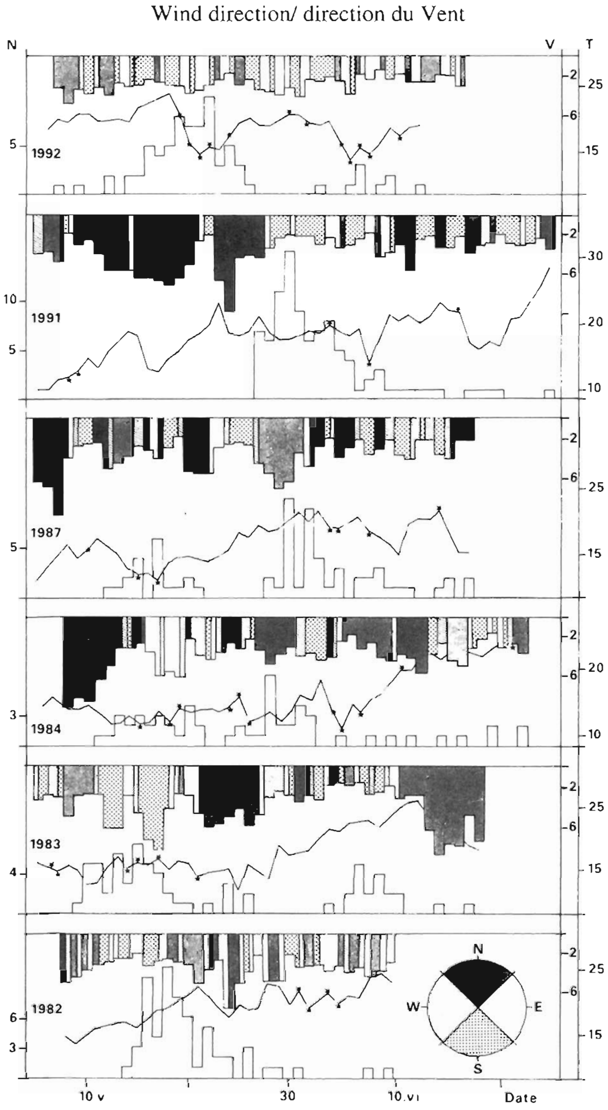


Figure 5. Influence des conditions climatiques sur la chronologie des pontes en 1982, 1983, 1984, 1987, 1991 et 1992. Le cercle indique la direction des vents. Un vent intermédiaire est représenté par l'accumulation des couleurs des vents qui l'encadrent. La vitesse (v) est donnée en mètres par seconde (m/s). Les températures (T, trait plein) sont exprimées en degrés Celsius. N = nombre d'oeufs; * = précipitations ≥ 1 millimètres. *Influence of climatic conditions on the timing of egg laying in 1982, 1983, 1984, 1987, 1991 and 1992. Circles indicate wind direction. An intermediate wind speed is displayed with graded colours. Speed (v) is given in metres per second (m/s). Temperatures (T, continuous line) are expressed in degrees centigrade. N = number of eggs; * = rainfall ≥ 1 millimetres.*

conséquence présumée un début de ponte étalé, qui n'augmentait qu'après l'apparition de vent de secteur ouest et est . Durant ce mois, nous n'enregistrerons pas de température supérieure a 25° C (moyenne de température la plus basse depuis 1946. Les précipitations étaient importantes du 15 au 25 mai (du 136e au 146e jour de l'année, il est tombé 127,6 mm de pluie), avec présence d'orages (10) et de grêles (5). Si le faible nombre de jours de vent fort (5) n'est visiblement pas à l'origine de l'étalement de la ponte, en revanche, la présence d'une periode pluvieuse associée à une baisse des températures sur la totalité du mois donnent à 1984 la plus longue période de ponte (43 jours).

En 1983 et 1987 nous avons observé une séparation en deux parties de la période de ponte (Figures 4 et 5). Les mois de mai et juin 1983 étaient déficitaires en précipitations, avec des températures le plus souvent supérieures à 15°C. En revanche, si le vents de secteur nord étaient peu présents en début de ponte, leur apparition le 21 mai ont entrainé un blocage de la ponte. En 1987, les conditions climatiques étaient différentes, avec un mois de mai frais, caractérisé par deux périodes froides du 3 au 7 mai et surtout du 13 au 24 où les températures minimales sous abri étaient souvent inférieures à 10°C. Du 9 au 24 mai les températures étaient le plus souvent inférieures à 15°C et ne remontaient à 20°C qu'à partir du 30 mai. La premiére décade de juin accusait elle aussi une baisse sensible des températures du 8 au 10 juin. La vitesse du vent entre le 11 et le 26 mai n'était que de 2,7 m/s et son action était moins influente que la baisse de la température qui perturbait le déroulement de la ponte avec un arrêt complet du 22 au 27 mai. Ces deux années semblent donc bien illustrer un effet important de la présence de vent de secteur nord sur le déroulement de la ponte. L'analyse comparative des deux pics de ponte qui encadrent les deux phénoménes météorologiques de 1983 et 1987 montre des pertes sensiblement identiques entre la ponte et l'éclosion de chacun des pics de ponte. En revanche, des pertes plus importantes entre la ponte et l'envol apparaissent en 1983 (39,5% et 80,0%) comparativement à 1987 (26,4% et 30,4%). Ceci suggère qu'un phénomène qui tend à repousser les pontes peut également augmenter la mortalité, mais aussi qu'une baisse de témperature au moment de la ponte a des conséquences moins importantes que la présence d'un vent violent. Ce dernier agirait comme un facteur limitant pour l'entomofaune, unique source énergetique des femelles au moment de la formation de l'oeuf (Gory 1992).

Influence des facteurs météorologiques sur le comportement des oiseaux reproducteurs. L'analyse du rythme d'activité sur le nid, de la période prépositale à la ponte du dernier oeuf (Figure 6) nous montre que lors de conditions météorologiques normales, les reproducteurs passent plus de 61% de leur temps sur le nid (38.4% d'absence en 1986, 39,0% en 1988, nid 319). La baisse des températures enregistée en 1987 a modifié le comportement des oiseaux qui ne passaient plus qu'en moyenne 35,6% de leur temps sur le nid (nid 313: 74,4% d'absence, nid 317: 72,4%, nid 319: 56,0%, nid 322: 54,7%). Le nombre moyen d'entrées et de sorties de la cavité avant la premiére éclosion était lui aussi inférieur les jours de mauvais temps (voir la comparaison du rythme d'activité entre 1987 et 1992, années défavorables et 1986 année favorable, Tableau 2). La différenciation entre les durées d'incubation (temps de développement de l'embryon) et de couvaison (temps pendant lequel l'oiseua reste effectivement sur ses oeufs) de 1986 à 1988, n'a pas révélé de différences significatives entre les années considérées (Analyse de Variance à deux facteurs: Pour l'incubation; effet nid et effet année n.s., Pour la couvaison; effet année et effet rang n.s., Tableau 3).

L'élevage des poussins.

De 1980 à 1992, 52% des éclosions avaient lieu dans les premiére et deuxième décades de juin (dates extrêmes: 25 mai - 11 juillet, n = 676). Les éclosions se sont échelonnées sur une période minimale de 18 jours en 1982 et maximale de 49 Jours en 1990.

Influence des facteurs météorologique sur l'élevage des poussins. En région méditerranéenne, les mois de juin et juillet sont génèralement des mois chauds, secs et peu ventés. Notre analyse porte sur les années 1984 et 1992 qui ont présenté des écarts par rapport aux normales saisonnières. En 1984, la période d'élevage était caractérisée par des températures proches des normales en juin, légérement supérieures en juillet, des précipitations déficitaires et un nombre de jours de vent fort supérieur à leur nombre moyen. En 1992, les mois de juin et juillet étaient exceptionnellement pluvieux (nouveaux records depuis 1946 en juin, deux fois la normale en juillet) les températures étaient en dessous des normales en juin et au dessus en juillet

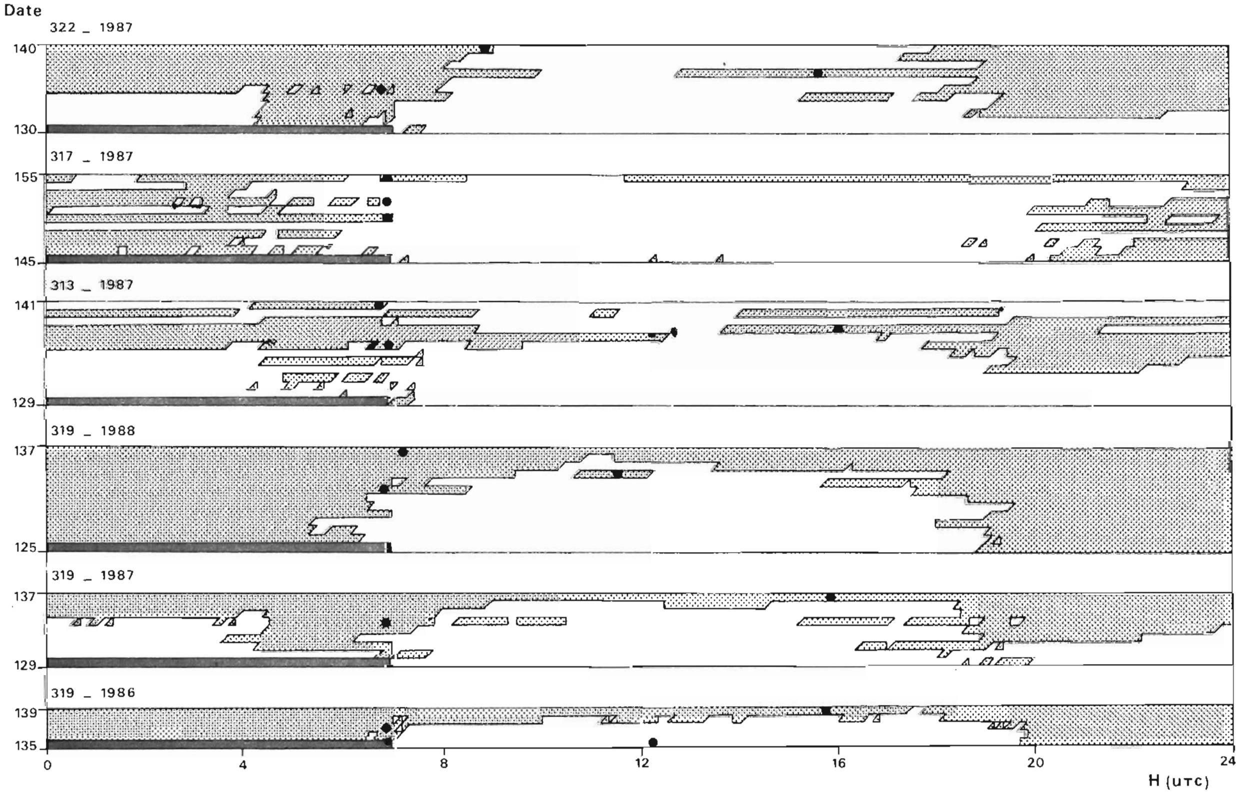


Figure 6. Evaluation du temps de présence (grisé) d'un Martinet noir sur son nid (Nid 319; 1986-1987-1988. Nids 313-317-322; 1987). En abscisse, les heures divisées par tranches de cinq minutes, en ordonnée, les jours de l'année. En blanc: absence d'oiseau, en noir: partie non comptabilisée. H : heure utc. • Ponte d'un oeuf. *Time presence (in grey) of an adult swift on the nestcup (Nest 319; 1986-1987-1988. Nests 313-317-322; 1987). On the x-axis, hours are divided into five-minute periods, the y-axis displays the days of the year. White: no bird present, Black: period not assessed. H: time utc.• = Laying of an egg.*

Tableau 2. Nombre moyen de contacts par jour enregistrés au nid du Martinet noir. Données cumulées de la période prépositale l'éclosion du dernier poussin. Activité I: Comparaison entre les années à conditions climatiques défavorables (1987 et 1992) et 1986 année favorable. Activité II: Activité les jours de mauvais temps en 1987 et 1992 (voir figure 5). n = nombre d'heures exploitées. *Mean number of contacts (i.e., entering or leaving the nest) per day. Data are cumulated from pre-laying to hatching periods. Activity I: Comparison between years with unfavourable climatic conditions (1987 and 1992) and years with good climatic conditions (1986). Activity II: Only days with weather conditions considered (years 1987 and 1992), see also figure 5. n = number of hours used for the analysis.*

ACTIVITE		ANNÉES					
		Bonne année		Mauvaises années			
		1986		1987		1992	
	Nids	317	319	317	319	317	319
I : nb contacts/jour	toutes dates confondues	12	10	11	7	11	13
n		960	1104	1032	1104	1008	816
II : nb contacts/jour	les jours de mauvais temps			10	6	8	9
n				168	408	240	288

(+3°C), le nombre de jours de vent fort restant faible. Les vents et les précipitations influencent l'évolution de la biomasse de la colonie et l'augmentation du poids moyen des poussins (Figure 7). Ainsi, en présence de vent de secteur nord sur une période supérieure a deux jours, correspond une baisse de la biomasse et du poids moyen, les vents de secteur sud semblaient eux, moins influents (Figure 7). La durée d'élevage ($\bar{X}$ = 40,7 jours (39-45), n=237, Gory 1991) se situe généralement dans une période peu pluvieuse sauf en 1992 où nous avons enregistré 163,6 mm de pluie en 40 jours. Les longues séries pluvieuses engendrent elles aussi une baisse des courbes de la biomasse et du poids moyen (Figure 7). En l'absence de pluie et de vent du nord et le jours qui suivaient une faible pluviosité, les deux courbes remontaient de manière spectaculaire (Figure 7). Pendant la durée de l'étude nous n'avons pas noté de baisse de températures pouvant engendrer des perturbations significatives au moment de l'alimentation des poussins. En revanche, nous avons constaté qu'une élévation anormale des températures était à l'origine des chutes des poussins (27 poussins agés de plus de 11 jours ont été récupérés avec des températures moyennes sous abri de 30,9°C).

Influence des facteurs météorologiques sur le comportement des oiseaux reproducteurs. L'analyse du rythme d'activité sur trois nids en période d'alimentation des jeunes a montré que la fréquence des entrées et sorties des adultes était supérieure les années favorables (28 et 33 contacts journaliers en 1986, 17 et 20 contacts les jours de pluie en 1992, 20 et 25 contacts les jours de vent du nord en 1984). L'évaluation du temps écoulé entre la sortie d'un oiseau et son retour au nid était en moyenne compris entre 86 et 95 minutes en 1986 (n=93 apports de nourriture), 127 à 137 minutes en 1984 (n=57 apports) et 131 à 132 minutes en 1992 (n=135 apports).

Discussion

Il a été démontré chez de nombreuses espéces, que l'âge des reproducteurs influe sur la taille des pontes (Blondel 1975, Kluijver 1951, Weitnauer 1947, 1980). Chez le Martinet noir, le nombre d'oeufs pondus est asujetti à une variation individuelle dont Lack (1954, 1956) a discuté la signification adaptative (Lack et Lack 1951), qui permet une production supérieure à la moyenne quand la nourriture est abondante. En présence de pontes précoces, Lack (1963, 1968) et Perrins (1970) expliquent un nombre d'oeufs inférieur au pontes plus tardives par le manque d'énergie nécessaire à la femelle pour produire la ponte moyenne optimale. Ainsi, le nombre d'oeufs pondus peut être limité en début de saison quand la nourriture est rare et les températures basses. En réalité, il faut considérer que la position geographique du lieu d'étude joue également un rôle dans l'accumulation d'énergie nécessaire à la femelle pour pondre. En régle générale, on assiste d'ailleurs à un cline dans la taille de ponte, avec la latitude, l'augmentation de la durée du jour qui en découle

Tableau 3. Données comparatives sur les durées de l'incubation et de couvaison (exprimées en heures) des oeufs de Martinet noir. Rg = rang de l'oeuf; $\overline{X}$ = Moyenne; σ = Ecart type; n = taille l'échantillon. Les moyennes et les données entre parenthèses sont exprimées en jours. Seules les valeurs significatives du F de Fisher (ANOVA) sont présentées.*Comparaison between length of incubation and length of brooding (expressed in hours) of clutches. Rg = rank of the egg; $\overline{X}$ = Mean; σ = Standard deviation, n = sample size. Data between brackets are expressed in days. Only significant F values are given (see text).*

NID	AN	Rg	DUREE		NID	AN	Rg	DUREE	
			Incubation	Couvaison				Incubation	Couvaison
319	1986	1	528 (22)	448,15 (19)	206	1988	1	528 (22)	422,05 (18)
		2	528 (22)	480,40 (20)			2	504 (21)	419,30 (17)
321	1986	1	576 (24)	443,05(18)	111	1988	1	552 (23)	506,25 (21)
		2	504 (21)	430,20 (18)			2	528 (22)	504,15 (21)
322	1986	1	528 (22)	463,40 (19)	115	1988	1	576 (24)	432,55 (18)
		2	480 (20)	415,25 (19)			2	528 (22)	413,05 (17)
313	1987	1	576 (24)	470,10 (19)	319	1988	1	528 (22)	494,35 (21)
		2	528 (22)	443,15 (18)			2	504 (21)	489,10 (20)
		3	480 (20	431,40 (18)			3	480 (20)	474,45 (20)
317	1987	3	480 (20)	475,25 (20)	3201	1988	1	624 (26)	462,20 (19)
							2	600 (20)	486,05 (20)
							3	552 (23)	493,50 (21)
319	1987	1	528 (20)	483,10 (20)					
		2	528 (22)	507,40					
					321	1988	1	528 (22)	473,45 (20)
3201	1987	1	480 (20)	435,15 (18)			2	504 (21)	472,10 (20)
		2	456 (19)	426,45 (18)			3	480 (20)	464,45 (19)

INCUBATION : $\overline{X}$ = 21,86 (19 - 26)
σ = 1,64 n = 29

Effet rang : F = 3,32 P = 0,04

COUVAISON : $\overline{X}$ = 19,21 (17 - 21)
σ = 1,17 n = 29

Effet rang : F = 3,32 P = 0,003

permettant un allongement du temps d'alimentation, excepté dans une zone à fortes instabilités climatiques (Koskimies 1950, Lack 1955, 1956). Rodriguez-Teijeiro (1980) a suggéré que la taille maximale des pontes (3 oeufs) a lieu en Europe Centrale et aboutit par deux gradients régressifs en direction du nord et du sud à des pontes à deux oeufs. La productivité moyenne annuelle d'un couple reproducteur dans le sud de la France (Tableau 4), nous situe en effet de manière intermediaire entre l'Espagne (X=2,32) et la Tchécoslovaquie (X=2,60 et 3,00 en 1981 et 1982; Vizyova et Janiga 1986). Les variations annuelles constatées tout au long de notre étude semblent imputables aux conditions météorologiques défavorables qui perturbent l'accumulation de réserves suffisantes pour la production d'oeufs. En période de conditions météorologique normales , O'Connor (1979) signale que la quasi totalité de la ponte a lieu sur un intervalle de 15 jours en Angleterre, de 12 jours en Espagne (Rodriguez-

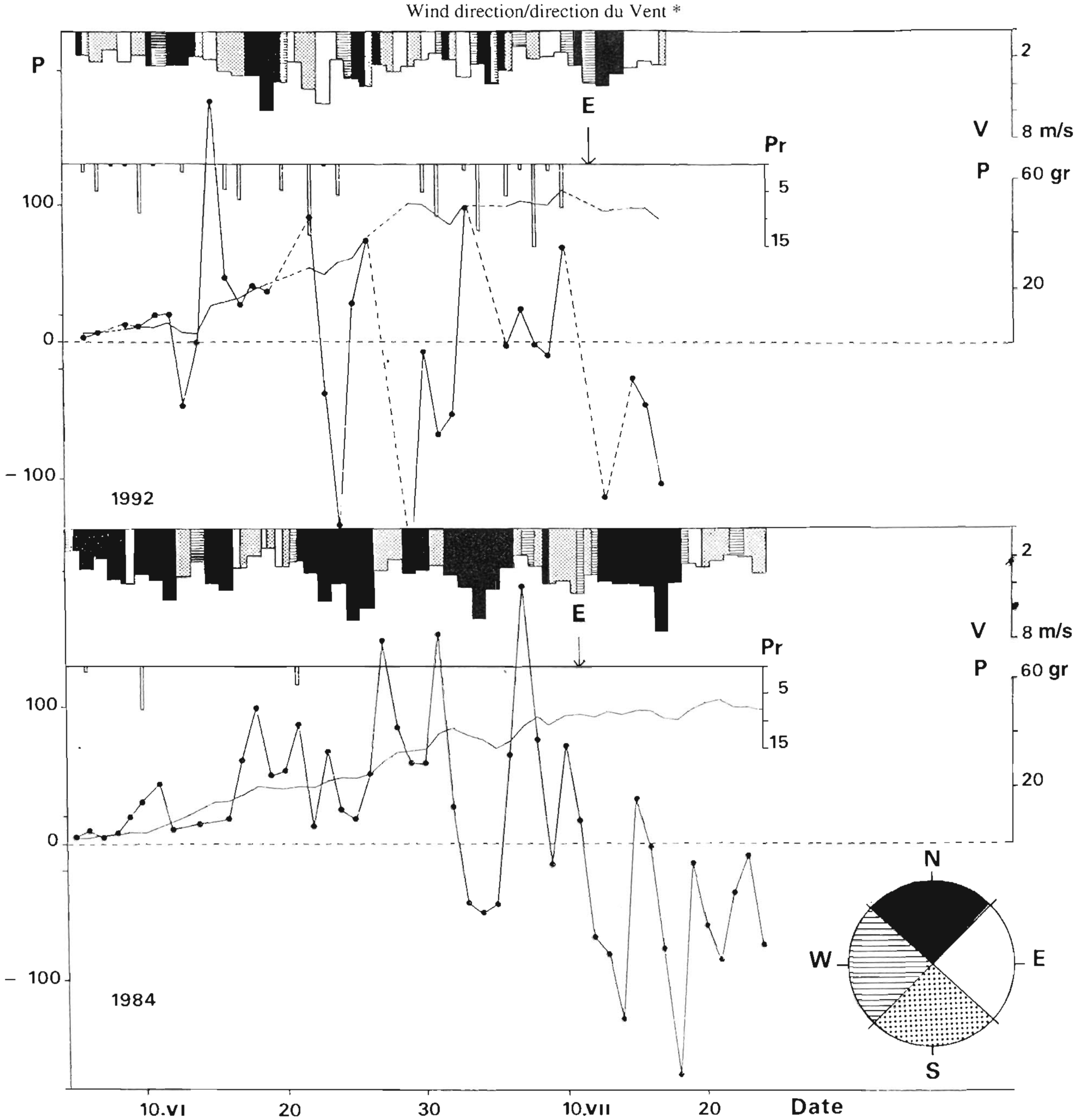


Figure 7. Influence des vents et des précipitations sur l'évolution de la biomasse de la colonie (•) et sur l'augmentation de poids moyen des poussins (trait plein). L'analyse porte sur 3364 données de poids récoltées en 1984 et 1992. Le cercle indique la direction des vents. La vitesse (V) est exprimée en mètre par seconde (m/s), le poids (P) en grammes, les précipitations (Pr) en millimètres. Ev = dates des premiers envols. *Influence of the wind and temperature on the biomass at the colony (•) and on the average chick growth (continuous line). The data consist of 3364 weights, taken between 1984 a 1992. Circles indicate wind direction. Wind speed (V) in m/s weight (P) in grs, rainfall (Pr) in millimetres. Ev = date of first departure of fledgings.*

Teijeiro 1980), par beau temps nous constatons nous aussi un regroupement des pontes, 50% des pontes à trois oeufs et plus ne précédent que de trois à quatre jours celles à un et deux oeufs (Gory 1992). En revanche, en présence de conditions défavorables, on note un rallongement de la période de ponte, les 50% de pontes à trois oeufs et plus précédent de 11 à 23 jours celles à un et deux oeufs. Notre étude montre que tout accident climatique retarde non seulement les dates de début de pontes mais aussi sa durée. En période de ponte, le facteur climatique le plus influent dans notre région est le vent de secteur nord-nord ouest (dépression sur la mediterranée) dont les rafales peuvent dépasser les 100 Km/heure (Sol 1985). Par ailleurs, on connait l'importance des grands phénomènes météorologiques, tels que les dépressions, sur l'alimentation des martinets (Koskimies 1947, Lack 1958), qui obligent les oiseaux à parcourir des distances importantes (Elkins 1983), rallongent les temps de chasse et modifient l'activité au nid. Si la période qui précède la ponte joue un rôle important sur son déroulement, on sait qu'en Angleterre la date moyenne de ponte est étroitement liée à la température de l'air des trois semaines qui précèdent la reproduction (O'Connor 1979). Les individus de nombreuses espèces ajustent leur taille de ponte à la quantité de nourriture disponible (Lack *et al.* 1957, Siivonen 1957, Perrins 1965, Ponce 1992). Chez le Martinet noir, le succès de reproduction est également dépendants des disponibilités alimentaires, elles même tributaires des conditions météorologiques. Le nombre moyen de poussins à l'envol de 1981 à 1992 varie de 1,25 à 1,79 poussins par nid. Les années qui le meilleur rendement n'ont pas subi de perturbations notables au cours de l'élevage. En revanche, les années 1983, 1984, 1991 et 1992 présentent des conditions météorologique défavorables.

Par beau temps, Gustafson *et al.* (1973, 1977) ont évalué la hauteur de chasse entre 1380 et 3600 métres et l'on sait par ailleurs que le Martinet noir est capable de chasser à basse altitude (Chinery 1983). Nous avons constaté au cours de cette étude que l'action d'un vent de secteur nord-nord ouest à partir d'un seuil compris entre 3,5 et 4 m/s sur une durée de deux jours suffit à modifier le nombre d'apports alimentaires (Gory 1987) et agit directement sur la survie du troisième poussin. Nous avons vu qu'une augmentation excessive des températures peut également entrainer un départ prématuré des jeunes engendrant une forte mortalité (Gory 1987).

L'effet des facteurs météorologique sur le succès de reproduction du Martinet noir est confirmé par notre étude, le succès de reproduction varie de 0,60 à 0,73 excepté les années où nous avons enregistré des conditions défavorables (en 1983, 1984 et 1992). L'année 1991, bien que marquée par un printemps froid qui a repoussé l'initialisation des pontes de plus de 20 jours, présente un bon indice reproducteur moyen (0,62). Nous avons constaté par ailleurs, que le retard pris au début de la saison de reproduction 1991, ne se retrouve pas au moment de l'envol des poussins. Compte tenu du raccourcissement de la saison de reproduction, et les oiseaux n'ayant matériellement pas eu le temps de reconstituer leur réserve (O'Connor 1979), le bon succès de reproduction de 1991 ne peut s'expliquer que par l'utilisation par compensation, du propre stock énergetique des reproducteurs. Même s'il ne dure que quelques jours d'après Martins et Wright (1993a, 1993b), nous suggèrons que l'affaibilissement qui en a résulté au moment du départ en migration, n'est probablement pas étranger à la diminution du nombre de reproducteurs l'année suivante. La campagne de baguage 1992 (voir Gory 1991 pour les méthodes), nous a en effet montré la formation de couples d'immatures (présents pour la première fois dans la colonie) ainsi que l'association d'individus bagués et d'immatures. Connaissant la fidélité au nid et au partenaire de ces oiseaux (Schierer 1962, Weitnauer 1980, Gory 1991), ceci suggère la perte

Tableau 4. Productivité moyenne d'un couple reproducteur sur la periode 1981 - 1992. X̄o = Nombre moyen d'oeufs pondus; X̄p = Nombre moyen de poussins à l'envol; X̄o/X̄p = Succès de reproduction; n1 = Nombre de nids avec reproduction; n2 = Nombre de nids occupés (n = 54 nids). *Breeding success parameters between 1981 and 1992 in the Common Swift. Xo = Mean clutch size; Xp = Mean number fledgings; Xo/Xp = Breeding success; n1= Number of study nests; n2 = Number of occupied nests (n = 54 nests).*

ANNÉES	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
X̄o	2,75	2,65	2.96	2,68	2,46	2,59	2,41	2,34	2,39	2,61	2,44	2,34
X̄p	1,65	1,74	1,35	1,55	1,79	1,73	1,70	1,40	1,61	1,61	1,51	1,25
X̄p / X̄o	0,60	0,66	0,46	0,58	0,73	0,67	0,71	0,60	0,67	0,62	0,62	0,53
n1	17	23	23	22	24	22	27	35	38	36	39	32
n2	32	35	37	35	38	38	43	44	45	47	47	48

"anormale" d'individus expérimentés et met en évidence les effect différés du refroidissement du printemps 1991.

Remerciements - Nous tenons à remercier le personnel de la Station de Météorologie Nationale de Nimes-Courbessac pour l'accès à ses archives, ainsi que R. Jeantet pour son aide. Nous remercions également V. Bretagnolle pour ses commentaires et suggestions lors de la rédaction de cet article.

Abstract - A preliminary analysis of 13 years data that were collected on the Common Swift (*Apus apus* L.) at colony of the Museum D'Histoire Naturelle de Nimes (Gard-France), have revealed that breeding success was related to climatic factors. We established that some characteristics of the mediterranean climate in southern France (e.g., wind), likely to affect entomofaun, and thus, the accumulation of the energy that is necessary for the production of eggs. Wind may also affect the initiation and timing of breeding. During the breeding period, climatic factors also affect chick growth. If high rainfall are rare under this climate in spring (1 case out of 13 years), we suggest that the important variations of temperatures have consequences on the chick's and also adult survival rates. In conclusion, this study suggest that some climatic factors (e.g., temperature, rainfall) have little affect, while others (especially north-north west wind), probably acting on food abundance and its accessibility, strong effects on breeding success of the Common Swift.

References

Andrewartha H.G. et Birch L.C. 1954. The distribution and abundance of animals. *Univ. Chicago Press, Chicago.*

Blondel J. 1975 La dynamique des populations d'oiseau. *In* Lamotte M. et Bourlière F. *La démographie des populations de vertébrés.* Paris, Masson: 147-232.

Boano G. et Cucco M. 1989. Breedind biology of the Pallid Swift (*Apus pallidus*) in North-Western Italy. *Gerfaut* 79: 133-148.

Chinery M. 1983. Les prédateurs et leurs proies. *Neuchâtel, Delachaux et Niestlé.*

Cody M.L. 1971. Ecological aspects of reproduction. *In* Farner D. S. & King J.R. *Avian Biology 1, Academic Press,* New York & London.

Di Castri F. 1981. Mediterranean-type shrublands of the world *in* Di Castri F. Goodall D.W. & Specht R.L. *Méditerranéan-type shrublands of the world* 11, Elsevier: 1-52.

Elkins N. 1983. Weather and bird behaviour. *T. & A.D. Poyser Calton.*

Farina A. 1980. Attivita diurna del rondone *Apus apus* (L.) nel periodo riproduttivo. *Avocetta* 4: 17-25.

Finlayson J.C. 1979. The ecology and behaviour of closely related species in Gibraltar (with special reference to swifts and warblers). *Thesis Univ. Oxford.*

Gory G. 1987. Influence du climat méditerranéen sur la reproduction du Martinet noir (*Apus apus* L.). *L'Oiseau et R.F.O.* 57: 69-84.

Gory G. 1988. Aménagements et perspective d'avenir pour la colonie Nimoise de Martinet noir (*Apus apus* L.). *Bull. Soc. Et. Sc. Nat. Nimes et Gard* 58: 71-79.

Gory G. 1991. Evaluation des effets du baguage sur une population nicheuse de Martinet noir (*Apus apus* L.). *L'Oiseau et R.F.O* 61: 91-100.

Gory G. 1992. Consequence d'une baisse de température sur la pont du Martinet noir *Apus apus. Alauda* 60: 41-47.

Gory G. et Jeantet R. 1986. Un actographe simplifié. Application au sexage du Martinet noir (*Apus apus* L.) *Bull. Soc. Et. Sc. Nat. Nimes et Gard* 57: 44-45.

Gory G. et Jeantet R. 1988. Un détecteur de chaleur simplifié Application à l'étude de la couvaison du Martinet noir (*Apus apus* L .) . *Bull. Soc . Et . Sc . Nat . Nimes et Gard* 58: 81-83 .

Gustafson T. Lindkvist K. et Kristiansson K. 1973. New methods for mesuring the flight altitude of birds . *Nature* 244 :112-113 .

Gustafson T. Lindkvist K. Gotborn L. et Gyllin R. 1977. Altitudes and flight times for swifts *Apus apus* (L.). *Ornis Scand.* 8:87-95.

Koskimies J. 1947. On movements of the swift, *Micropus a. apus* L. during the breeding season. *Ornis Fennica* 24: 106-111.

Koskimies J. 1950. The life of Swift, *Micropus apus* L., in relation to the weather. *Ann. Ac. Sc. Fenn.* 4, *Biol.* 15(A): 1-151

Kluijver H.N. 1951. The population ecology of the Great Tit *Parus m. major* L., *Ardea* 39: 1-135.

Lack D . 1954 . The natural regulation of animal numbers. *Oxford University Press.*

Lack D. 1955. The summer movements of Swifts in England. *Bird Study* 2: 32-40.

Lack D . 1956 . Swifts in a tower. *Methuen, London .*

Lack D. 1958. Weather movements of swifts 1955-57. *Bird Study* 5: 128-142.

Lack D . 1963 . Cuckoo hosts in England . *Bird Study* 10: 185-202 .

Lack D. 1968. Ecological adaptations for breeding in bird. *Methuen, London.*

Lack D. et Lack E. 1951. The breeding biology of the Swift *Apus apus. Ibis* 93: 501-546.

Lack D. Gibb J. et Owen D.F. 1957. Survival in relation to brood-size in tits. *Proc. Zool. Soc.* London 128:313-326.

Malacarne G. et Cucco M. 1991. Chick mortality and hatching asynchrony in the Pallid Swift *Apus pallidus. Avocetta* 15:19-24

Martins T.L. et Wright J. 1993a. Cost of reproduction and allocation of food between parent and young on the swift (*Apus apus*). *Behav. Ecology* 4: 213-223.

Martins T.L. et Wright J. 1993b. Brood reduction in response to manipulated brood sizes in the common swift *(Apus apus) Behav . Ecol . Sociobiol. .* 32: 61-70 .

Nahal I. 1981. The mediterranean climate from a biological viewpoint, *in* Di Castri F. Goodall D.W. & Specht R.L Mediterranean-type shrublands. Ecosystems of the world. *11, Elsevier: 63-86.*

Nicholson A.J. 1954. An outline of the dynamics of animal populations. *Aust. J. Zool.* 2: 9-65.

O'Connor R.J. 1979. Egg weights and brood reduction in the European Swift *(Apus apus). Condor* 83: 133-145.

Perrins C. M. 1965. Population fluctuations and clutch-size in the Great-Tit. *Parus major. J. Anim. Ecol.* 34: 601-647.

Perrins C. M. 1970. The timing of birds breeding seasons. *Ibis* 112:242-255.

Ponce F. 1992. Régime alimentaire du Tétras lyre *Tetrao tetrix* dans les alpes Francaises. *Alauda* 60:260-268.

Ribaut J. P. 1964. Dynamique d'une population de Merles noirs *Turdus merula. Rev. Suisse de Zool.* 71:815-902.

Rodriguez de los Santos M. et Rubio Garcia J. C. 1986. Biology and biometry of the Pallid Swift *(Apus pallidus)* in southern Spain. *Gerfaut* 76:19-30.

Rodriguez-Teijeiro J. D. 1980. Contribution al conocimiento de la biologia y etologia de la especie Apus apus *(L. 1758). Tesis, Barcelona.*

Schierer A. 1962. Contribution à l'étude du Martinet noir *(Apus apus). Bull. Ass. Phil. Alsace-Loraine* XI, (1862-1962): 148-153.

Siivonen L. 1957. The problem of the short termed fluctuations in numbers of tetraonids in Europe. *Pap. Game Res.* 17: 1-44.

Sol. B. 1985. Application d'un résau météorologique automatique à la prévision des risques de feux de forêt en région méditerranéenne. *Rev. Palais de la Découverte* 13, 130:201-212.

Solomon M. E. 1959. The meaning of density-dependance and related concepts. *Proc. 15 th Int. Congr. Zool.* London 1958: 784-787.

Taylor L. R. 1963. Analysis of the effect of temperature on insects in flight. *J. Anim. Ecol* 32: 99-117.

Thibault J. C., Brunstein D., Pasquet E. et Guyot I. 1987. La reproduction du Martinet pale (*Apus pallidus*, Shelley) sur les îlots satellites de la Corse: ses relations avec les facteurs climatiques. *Rev. Ecol. (Terre Vie)* 42: 277-296.

Vizyova A. et Janiga M. 1986. Notes on the ecology of Common swift (*Apus apus* L., 1758) in Brastilava. *Biologia (Brastilava)* 41: 151-161.

Weitnauer E. 1947. Am neste des Mauerseglers *(Micropus a. apus* L.) *Orn. Beob.* 44 : 133-182.

Weitnauer E. 1980. "Mein Vogel". Aus dem Lebem des Mauerseglers Apus apus. *Oltingen bl.*

Avocetta N° 17: 189-197 (1993)

Survival rate and mate fidelity in the Pallid Swift *Apus pallidus*

GIOVANNI BOANO[(1)], MARCO CUCCO[(2)], GIORGIO MALACARNE[(2)] and GUALTIERO ORECCHIA[(2)]

[(1)] *Museo Civico di Storia Naturale, Casella Postale 89 - 10022 Carmagnola*
Present address: I.P.L.A., Corso Casale, 476 - 10132 Torino
[(2)] *Dipartimento di Biologia Animale, Via Accademia Albertina, 17 - 10123*

Abstract - Survival and fidelity both to the mate and to the nest were studied in a colony of Pallid Swifts in Piedmont (NW Italy). An overall adult survival rate of 75%, as estimated by the Jolly-Seber and related methods, was found in the whole colony. Females and males showed no differences in survival rate; the mean life span as an adult was 3.61 years. Adult breeding birds showed a wide range of strategies: some were faithful to the nest cavity or to the partner for many years, but a considerable percentage of birds changed cavity and/or partner year after year. Compared with other European species of swifts, the Pallid Swift seems to be characterized by slightly lower survival and less intense mate and nest fidelity.

Introduction

Long term studies of colonial birds have shed light on many aspects of life-history and mating system theories (Newton 1989). Among the pioneering studies, Lack's work on population dynamics has had a major impact. In this view (Lack 1954, 1966), mortality and its relation to ecological factors play a critical role in the regulation of animal numbers.

In ornithology, mortality (or survival) estimates have traditionally been derived from analyses of ring recoveries (i.e. recoveries of marked birds, usually found dead, made by the general public from a large geographic area: Haldane 1955, Brownie *et al.* 1985). Currently, they are also being derived from analyses of recaptures or resightings of live marked birds (i.e. recaptures of marked birds, usually made at a local study area) in association with proper stochastic open-population models (Cormack 1964, Nichols *et al.* 1981, Seber 1982, Clobert *et al.* 1985, Pollock *et al.* 1990).

A major problem in estimating mortality from capture recapture studies at a local site arises from the possibility of permanent emigration: if a significant part of the population, although alive, does not return to the sampling site in the subsequent sampling times, then mortality estimates will be positively biased. Thus bird species known to be strongly philopatric are more suitable for investigation by this last method. In any case estimates derived from capture-recapture experiments have to be regarded as minimal survival values.

Survival estimates arising from local studies are valid for a clearly defined population, which is not the case in large-scale recovery studies. At such a local scale other biological phenomena can also be easily studied, thus providing good opportunities to test hypotheses of ecological and methodological interest (Clobert *et al.* 1985).

Long-term studies of Holarctic swifts have been extant since the middle of the century. In particular, the Common *Apus apus* and Alpine *A. melba* Swifts have been extensively studied (Lack 1956, Weitnauer 1947, Arn 1960, Koskimies 1950), whereas there are no such long term studies of the more southern Europe Pallid Swift *A. pallidus*. This last species differs from the other two mainly in one aspect of its reproductive biology, the laying of a second clutch, which occurs in about 30% of the pairs nesting in spring (Cucco *et al.* 1992). As result, the laying period is protracted until very late in the season; eggs are found in September and chicks are fed for the whole of October and sometimes November (Boano and Cucco 1989). A survey of European swift studies (data from Cramp 1985) shows that *Apus* species are long-lived and survival, calculated on ring recoveries, is high. It ranges in the Common Swift from 84% (Oxford) to 76% (other areas in Britain), while in the Alpine Swift survival is 79% (Switzerland). First-year swifts are much less likely to survive than adults; their

Accepted 29 December, 1993

survival rate is only 24% in the Alpine Swift, and similar values have been reported for the Common Swifts. The only study of survival in a Pallid Swift colony was in Gibraltar (Finlayson 1979), where a lower rates have been found (74% survival in adults and 33% in first-year birds).

Adult European swifts are well known to be highly philopatric, so they are suitable for survival analysis by capture-recapture experiments. Partners in a pair have been found together for 12 years. Fidelity has been demonstrated both to the nest-cavity and to the previous partner. Also in the Pallid Swift, marked fidelity to colony and nest site have been described (Finlayson 1979).

In this paper we summarize 17 years of observations in a colony in Piedmont (NW-Italy). Data are reported on colony consistency, survival rate and mate fidelity.

Methods

The study was carried out from 1976 to 1992 in the town of Carmagnola (NW-Italy). The climate in the area is continental and specifically defined as "sub-litoraneo Padano" (Mennella 1967). Rainfall reaches one peak in May and another in November. From June to late October the weather is generally favourable, with warm temperatures and few rainy days.

The colony is situated in an old building and, during the study period, we observed a yearly average of 13 pairs (min 7, max 19. Figure 1). The nests were easily reached and inspected from inside the building. Nest-cavities were numbered (N=22) and inspected almost fortnightly (from 1976 to 1986) or daily (from 1987 to 1992). From 1987, all young and nearly all the adults were marked with metal rings of the Italian Ringing Scheme; before 1987 ringing effort was not so intensive.

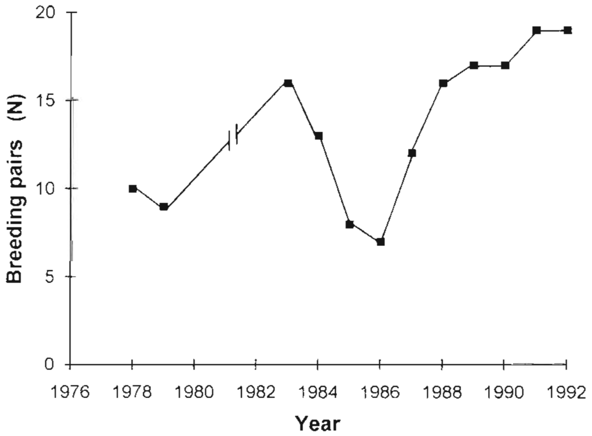


Figure 1. Number of first clutches observed in the Carmagnola study colony.

Nest and mate fidelity

The Pallid Swift typically lays a first clutch in May-June, and some females lay a second clutch in August-September (Boano and Cucco 1989). In this paper we will only analyze nest and mate fidelity in the first clutches, because the adults were not regularly captured in autumn during the second breeding period. The identity of the individuals nesting in the different cavities was ascertained by capturing the adults at night. To avoid disturbance and the possibility of nest-abandonment, the captures of adults took place when their nestlings were at an age of 40 days, which is near the fledging date. Birds were immediately released after the usual ringing operations and measurements of wing lenth and weight.

Sex of the adults was ascertained only in the years from 1987 to 1992. In this period the breeding Pallid Swifts were individually marked by bleaching a few feathers on their back (Malacarne and Griffa 1987), and the behaviour at the nest was monitored by videocameras (Malacarne *et al.* 1992). Sex was determined by examining the videotapes recorded during the days of laying, and detecting which of the two parents laid the eggs.

Breeding parameters

The laying date in each year is influenced by the weather conditions (Cucco *et al.* 1992). In order to investigate differences in the laying date between classes of adults (those that did or did not change nest or mate), and to avoid the effect of weather, we calculated for each year the median date of laying in the colony, and then we calculated for each female the difference between her laying date and the median date for that year (i.e. the number of days earlier or later than the median).

Means and standard deviations were calculated on logtransformed values, when necessary, in order to correct for the errors caused by non-normal distributions (Fowler and Cohen 1992).

Clutch and brood sizes were ascertained from 1987 to 1992 by daily inspections of the nest-cavities. Chicks which exhibited regular growth and left the nest after 40-45 days, were considered successfully fledged.

Survival rate

Demographic parameters were estimated using the Jolly-Seber and related stochastic models (Jolly 1965, Seber 1965, Brownie *et al.* 1985, Pollock *et al.* 1990).

These models include parameters for both survival (*s*) and capture probabilities (*p*). Survival probability is the probability that a bird which is alive during the period *i* will still be alive and in the sampling area during the period *i*+l. As with all capture-recapture sampling, the complement of survival probability estimates (l-*s*) includes both mortality and permanent emigration.

Capture probability is the conditional probability that an individual will be caught during period *i*, given that the individual is alive and in the relevant area at the time of sampling. Survival estimates based on these models differ from estimates which equate survival and recapture rates, because the models explicitly include the possibility that an individual is alive and in the population being sampled, but simply not caught. In contrast, methods which equate survival and recapture rates require the assumption that capture probability is 1, and they yield unbiased estimates of survival only in the very unusual condition in which every marked animal still in the population is actually caught (Nichols and Pollock 1983). Other parameters estimated by the models are the number (N) of birds present in the population in each sample period, and the recruitment (i.e. the number of birds entering the population between sample period *i* and sample period *i*+l).

The basic assumptions of the Jolly-Seber model are discussed by Seber (1982), the most important being:

(1) every bird present in the population at the time of sampling in period *i* has the same probability of being captured;

(2) every marked bird present in the population immediately after sampling period *i* has the same probability of surviving until period *i*+l ;

(3) marks are not lost or overlooked;

(4) all emigration is permanent;

(5) the sample is instantaneous (i.e. the sampling time is negligible in relation to the intersample period).

Biased estimates of the parameters of interest may result from any departure from the above assumptions. Unfortunately, heterogeneity among individuals in either survival or capture probabilities likely affects animal populations (Johnson *et al.* 1986). If survival probabilities vary among individuals, then estimates will also be biased. If both capture probabilities and survival probabilities vary among individuals, and are correlated, the captured animals will not be representative of the general population with respect to survival rate. Heterogeneity within a population can arise from several sources, some of which are often associated with a measurable variable such as age or sex. We were forced to study only adult birds because of the very low philopatry of the young. We were, however, able to test sexual differences in survival because most birds were sexed at laying. Our data were collected each year in July (a few in June and August), to satisfy assumption 5.

All the estimate were obtained using the computer programs JOLLY (Pollock *et al.* 1990). These programs provide parameter estimates under the basic Jolly-Seber model (Model A) and other related models which either generalize or further restrict assumptions about capture and survival probabilities (assumptions 1 and 2; Table 1). The programs also provide goodness-of-fit tests and specific tests for individual assumptions. The input format adopted here consists of the capture histories of all the birds, coded with 0 (not captured in the sample period) or 1 (captured at least once in a sample period).

The mean life span as an adult (MLS) was calculated, according to Brownie *et al.* (1985), as: MLS=l/-log(*s*).

Results

Survival rate

The number of adult Pallid Swift ringed per year was on average 13, for a total of 78 birds.

Table 1. Summary of models provided in the JOLLY computer program.

Models *	Models **	Definitions
A	*st, pt*:	standard Jolly-Seber model, permitting time specific capture and survival probability;
B	*s, pt*:	reduced-parameter model with time specific capture probability, but survival probability assumed to be constant;
D	*s, p*:	reduced-parameter model with constant capture;
2	*st*, s^*, *pt*:	the most general model, similar to model A, but permitting also different survival probabilities for newly ringed birds (s^*) versus previously ringed birds.

* After the notations of Pollock *et al.* (1990).
** After the notations of Clobert *et al.* (1985).

We first consider the survival probabilities of females (N=32) and males (N=21) separately (Table 2). JOLLY's estimate under model A was the only one appropriate for the female data, even though model D would be acceptable, and more precise, for males. The values estimated by model A for the two sexes are 0.88 and 0.85 respectively.

Table 2. Mean adult survival rates of the Pallid Swift under model A (sexed birds).

	s	S.E. (s)	p	S.E.(p)
Females	0.884	0.052	0.815	0.159
Males	0.852	0.056	0.594	0.146

Survival rates and capture probabilities of females and males, compared with the z test (Brownie *et al.* 1985), showed no significant differences ($z(s)=0.416$ and $z(p)=1.02$, P=n.s.). Therefore, for further analysis we lumped together all the adult recoveries (females and males plus non-sexed birds, N=78). In this case model D is not rejected (Table 3); nevertheless, annual variation in survival rate appears to be very likely for the Pallid Swifts, thus we believe model A (Table 3) better describes survival in our colony. The goodness-of-fit tests (χ^2=4.73, d.f=4, P=0.316 n.s.) suggest no strong violations of the assumptions of the Jolly-Seber model. The survival rate estimate (0.749) is lower than those calculated for sexed birds; these findings will be discussed below.

The population size estimates are shown in Table 4. The mean number of males was slightly less than that of females, which resulted from the fact that captures were done at the end of the breeding period for each nest, when frequently only one parent spent the night in the cavity.

Table 3. Adult survival rates of the Pallid Swift (all birds).

Model D

s = 0.749 S.E. (s) = 0.050

p = 0.653 S.E. (p) = 0.005

95% conf. interval of s = 0.651-0.846.

Model A

Year	s	S.E.
1987	0.754	0.186
1988	0.838	0.105
1989	0.940	0.143
1990	0.500	0.114
Mean	0.758	0.058

The estimated population of the colony was about 40 individuals (Table 4), a value which is greater than the sum of sexed females and males because each year some swifts were captured but could not be sexed.

The mean life span as an adult was 3.46 years. The Pallid Swifts can nest for the first time at the age of two as indicated by two cases of birds ringed as nestlings, and retrapped during reproduction. Longer pre-reproductive periods of three to four years have been reported for the Common Swift (Perrins 1971) and cannot be ruled out for Pallid Swift as well.

Nest-cavity fidelity

Adults did not show a strong fidelity to the nest cavity: on average 29.2% of the birds that were present and alive the following year changed cavity (Figure 2) . There was no significant difference between females (36.3%) and males (27.3%) in the number of birds changing nest sites (χ^2=0.70, d.f.=l; p=n.s.). The greatest nest fidelity was exhibited by two females and one male which utilized the same

Table 4. Population size estimates (values calculated by the Jolly program: model D for the whole population and males, model A for females).

Year	Population size N	Population size s.e.	Females N	Females s.e.	Males N	Males s.e.
1988	33.2	4.95	10.0	–	11.3	2.08
1989	45.0	5.09	19.7	2.0	14.8	1.75
1990	38.8	3.55	23.6	5.0	13.1	1.29
1991	47.9	5.94	16.0	–	11.5	1.54
1992	44.4	6.35	–	–	14.1	2.33
Model D mean	41.8	8.52	17.3	–	13.0	2.66
Model A	36.3	3.33				

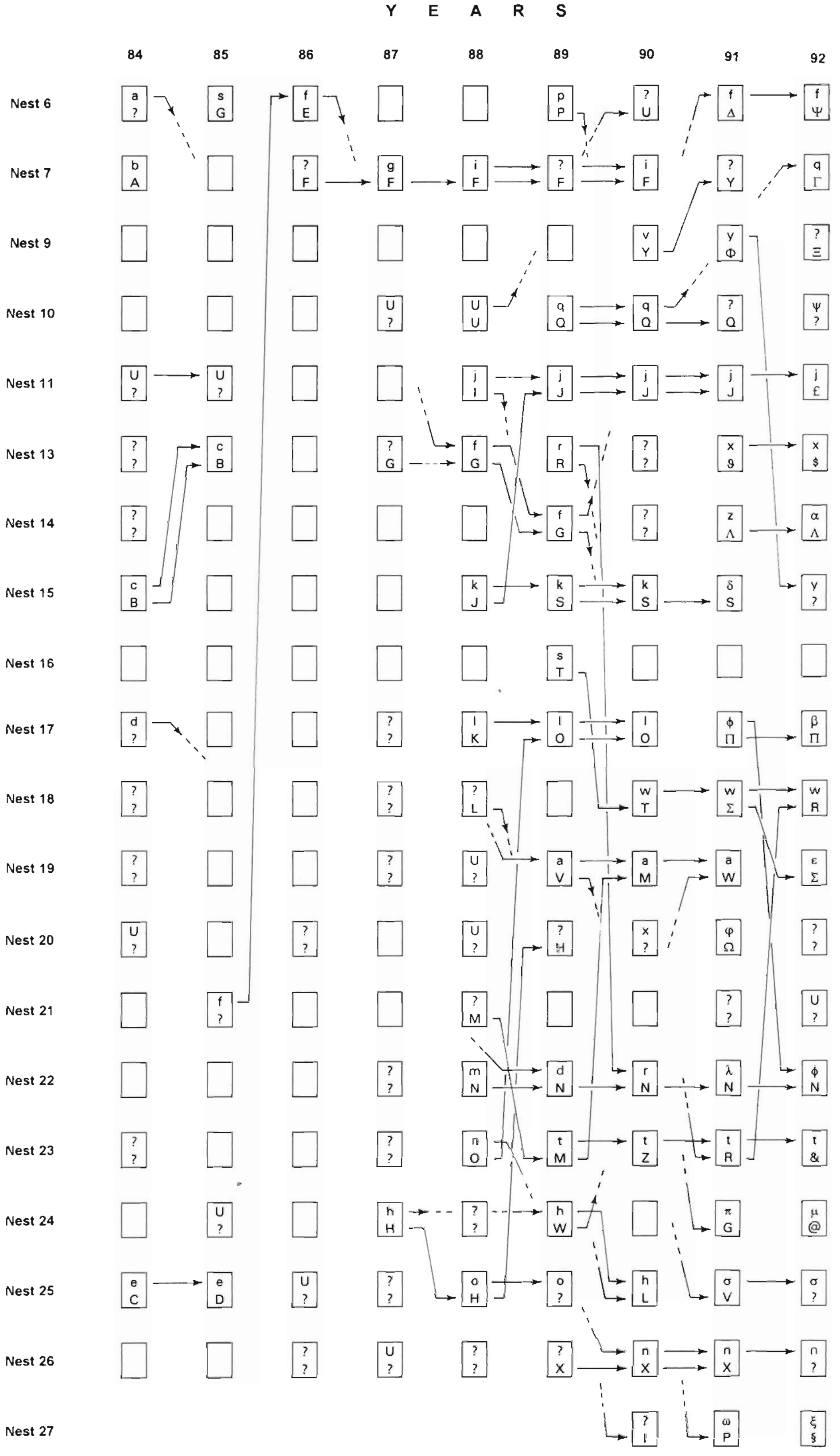


Figure 2. Cavity and partner fidelity in the Carmagnola colony.

□ = nest cavity

Capital letters = marked birds, females

Lower case letters = marked birds, males

U = marked birds, unsexed

? = not caught birds.

cavity for at least five years, even though their partner changed during this period.

There was a difference in laying date between birds which changed cavity or did not (Mann-Whitney test: U=258, N=60; p<0.036). Laying occurred 2 days earlier than the median date in birds nesting in the same cavity, but 0.5 days after the median date in birds which changed nest-cavity (Figure 3).

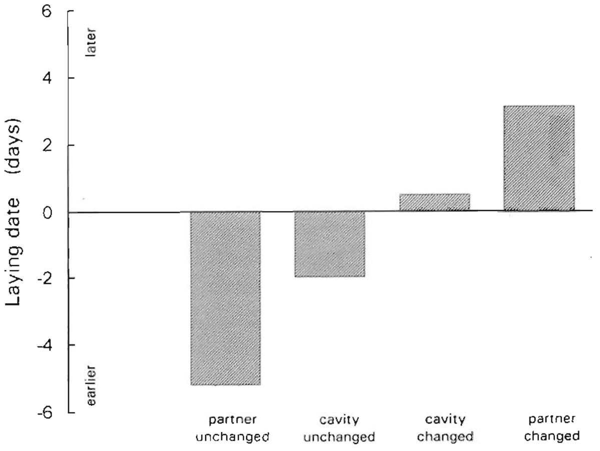


Figure 3. Median laying dates in birds changing or not changing the mate or the cavity.

The clutch size did not vary (U=120, N=30, p=n.s.) between females changing (2.7±0.48 eggs) or not changing (2.9±0.31 eggs) the cavity (Figure 4). A similar result was found (U=68, N=28, p=n.s.) in the comparison of the females paired either to males that changed (2.8±0.41 eggs) or did not change (2.9±0.35 eggs) the cavity. In comparison to the previous year, there was a slight, but not significant, increase in the clutch size both for cavity-changing and non-changing females (+0.17 and +0.29 eggs, respectively; U=46, N=19, p=n.s.), and in females paired either to cavity-changing or non-changing males (+0.21 and +0.29 eggs, respectively; U=52, N=21, p=n.s.).

The number of young successfully fledged was not significantly different (mean values ranging from 2.3 to 2.5 young/nest) between females who changed or did not change the cavity (U=70, N=26, p=n.s.), nor between females paired either to males who changed or did not change the cavity (U=39, N=22, p=n.s.). In comparison to the previous year, there was a slight, but not significant, increase in the breeding success both in cavity-changing and non-changing females (+0.25 and +0.86 young/nest, respectively; U=49.5, N=19, p=n.s.), and in females paired either to cavity-changing or non-changing males (+0.29 and +0.86 young/nest, respectively; U=58, N=21, p=n.s.).

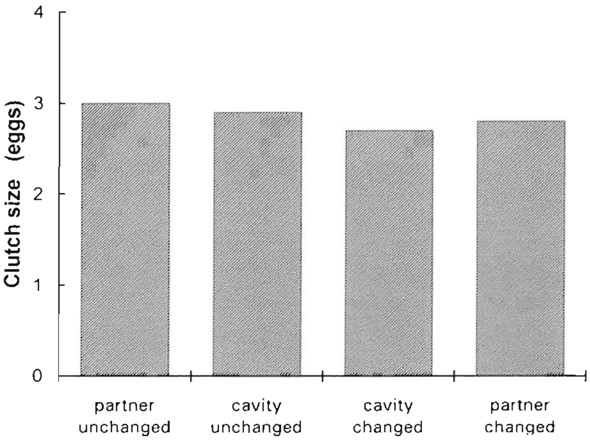


Figure 4. Mean clutch size in birds changing or not changing the mate or the cavity.

Mate fidelity

Adults did not show a high fidelity to their mates: on average the partner was changed by 58.3% of the birds whose partner was present and alive the following year (Figure 2). The greatest mate fidelity was exhibited by a pair of birds found together for three years. The opposite was shown by a male who, in the period 1985-92, nested successively in 5 different cavities and paired with 4 different females. Mate fidelity was not correlated to cavity-fidelity: in only one case, a bird that changed cavity moved together with the partner of the previous year, while in the remaining cases the mate of the previous year either did not change cavity or moved to a different one (Figure 2).

There was a significant difference in laying date between birds with changed or unchanged mate (Mann-Whitney test: U=46.5, N=34; p<0.04). On average, layings occurred 5.2±1.0 days earlier than the median date in birds with unchanged mate, and 3.1±1.1 days later than the median date when the mate was changed (Figure 3).

The clutch size was not significantly different (U=59.5, N=29, p=n.s.) between females who changed (2.8±0.43 eggs) or did not change (3 eggs) mate from the previous year (Figure 4). Furthermore, the number of young successfully fledged was not different (mean values ranging from 2.8 to 3 young/nest) between females who changed or did not change mate (U=49, N=24, p=n.s.). In comparison to the previous year, there was a slight, but not significant, increase in the breeding success both in mate-changing and non-changing females (+0.25 and +0.86 young, respectively; U=49.5, N=19, p=n.s.).

Discussion

Our estimates of survival in the Pallid Swift are based on the assumption that the adults show strong breeding philopatry. This is in accord with our observations (very many breeding adults have been recaptured year after year) and with all the long-term studies of European swift populations conducted to date (Cramp 1985).

The Pallid Swift survival rate calculated in this study does not differ from the estimates from Gibraltar. Adult survival in the three European swifts (Table 5) ranges from 74% to 85%. Pallid Swift values suggest that this species may suffers a higher mortality than its congeners. The estimated average life span of the Pallid Swift as adult (3.61 years) is, in consequence, lower than the values calculated for the Common Swift (3.64-5.73 years). On the other hand, given the considerable observed degree of variation between years, we believe that the aggregate standard error computed by the program and reported here may substantially underestimate the true uncertainty.

We did not find a sex difference in survival rate. This is in accord with some studies on birds in Britain (Dobson 1987), and on other colonial birds (e.g. Fulmar *Fulmarus glacialis*, Dunnett and Ollason 1978; Laysan Albatross *Diomedea mutabilis*, Fisher 1975; Short-tailed Shearwater *Puffinus tenuirostris*, Wooller *et al.* 1989). Sexual differences, however, have been shown in a few species in Britain (Dobson 1987, Coulson and Wooller 1976), and in another aerial feeder, the House Martin *Delichon urbica* (Bryant 1979).

Two results reported here must be considered critically: 1) the lower probability of capturing males than females could be due to a higher tendency of males to fly away from the nest during ringing operations, at night; 2) the higher survival of sexed birds vs the other birds could be due to: (a) a bird which survives for a longer period of time, and thus returns many times to the colony, will be more likely to be sexed than a bird which dies after only one or a few seasons; (b) the presence of immature birds which visit the monitored cavities only a few times. In the Pallid, Common and Alpine Swifts, these first-year non-breeding birds are known to have a lower survival rate than adults (Finlayson 1979, Perrins 1971, Glutz and Bauer 1980).

The estimated size of the colony (c. 20 pairs) is higher than the average values reported in Gibraltar, where 50% of the colonies were of less than 10 pairs (Finlayson 1979), but it is similar to those reported in North Italy (Boano 1979, Boano and Cucco 1988) and France (Yeatman 1976).

Mate and nest fidelity are high in the Common and Alpine Swifts (Weitnauer 1980, Arn 1960), as is the case in the majority of monogamous colonial birds (review in Newton 1989 and Clutton-Brock 1988). Contrary to the current belief (Cramp 1985), Pallid Swifts did not show, in our colony, strong fidelity to the mate or to the nest-cavity.

In birds, pairs showing high mate fidelity have higher breeding success (Coulson and Thomas 1985). This advantage can be due, among other factors, to the breeding earlier in the season of previously matched individuals. In fact, as a rule in the temperate zone, females laying earlier have a higher breeding success (Perrins 1970). Also in the Pallid Swift, there is a tendency to lay larger clutches early in the season (Cucco *et al.* 1992). In this study, faithful pairs initiated egg-laying earlier (on average by about a week), but this was not sufficient to induce significant differences in clutch size, hatching or fledging success compared with non-faithful pairs.

In conclusion, the Pallid Swift has a slightly lower survival rate and lower mate/nest fidelity than the two

Table 5. Estimates of the survival rates (*s*) in Pallid, Alpine and Common Swift, made with ringing recoveries (a) or recaptures at a breeding colony (b).

	(*s*)	S.E.	N	locality	years	method	Reference
Pallid	0.74	–	–	Gibraltar	1973-77	–	Finlayson 1979
	0.76	0.06	78	Italy	1976-92	Jolly	This study
Alpine	0.79	–	–	Switzerland	->65	–	Glutz & Bauer 1980
Common a)	0.79	–	–	Britain	1954-66	Haldane	Perrins 1971
	0.76	0.025	111	Britain	1966-78	Haldane	Dobson 1983
	0.808	0.033	–	Britain	1956-76	Brownie MO	Baillie & Green 1987
b)	0.84	–	22	Oxford	1965-66	Haldane	Perrins 1971

other European species of *Apus*. Moreover, considering that the Pallid Swift frequently has two clutches per season (Boano and Cucco 1989), one may say that in a traditional life-history categorization (Pianka 1970) this Mediterranean species seems more "r-oriented" than *Apus apus* and *Apus melba*. In this light, the findings on European swifts seem to contradict the tendency, widespread among birds, for an increase in clutch size and mortality with increasing latitude (Cody 1966).

Acknowledgments - We would like to thank Fulvia Gaia for help in field work. David Bradley and Charles Collins make helpful suggestion on first draft of the paper. This research was funded by 40-60% MURST grants to G. Malacarne.

Riassunto - In una colonia di Rondone pallido si sono studiati dal 1976 al 1992 i tassi di sopravvivenza e di fedeltà al nido e al partner. Il tasso annuale di sopravvivenza stimato con il metodo Jolly-Seber è pari al 76% e non esistono differenze tra i sessi. La vita media da adulto è stimata in 3.61 anni.

Esiste molta variabilità riguardo alla fedeltà: alcune coppie sono fedeli per più di un anno a partner e cavità di nidificazione, ma molti individui cambiano il sito di nidificazione e/o, in misura ancora maggiore, il partner rispetto all'anno precedente.

In confronto con le altre due specie europee del genere *Apus*, il Rondone pallido appare essere caratterizzato da una sopravvivenza lievemente inferiore e da una minore fedeltà al partner e alla cavità utilizzata per la riproduzione.

References

Arn H. 1960. Biologische Studien am Alpensegler. *Vogt-Schild AG Verlag, Solothurn.*

Baillie S.R. and Green R.E. 1987. The importance of variation in recovery rates when estimating survival rates from ringing recoveries. *Acta Ornithologica* 23:41-60.

Boano G. 1979. Il Rondone pallido *Apus pallidus* in Piemonte. *Riv. Ital. Orn.* 49:1-23.

Boano G. and Cucco M. 1988. Rondone pallido. In: (Mingozzi, Boano and Pulcher eds.) Atlante degli uccelli nidificanti in Piemonte e Valle d'Aosta, 1980-1984. *Museo Reg. Scienze Nat., Monografie* 8, Torino.

Boano G. and Cucco M. 1989. Breeding biology of Pallid Swift (*Apus pallidus*) in NW Italy. *Gerfaut* 79:133-148.

Brownie C., Anderson D.R., Burnham P.K. and Robson D.S. 1985. Statistical inference from band recovery data. A handbook. Second ed., U.S. Fish and Wildl. Service. *Resour. Publ.* 156: 1-305.

Bryant D. M. 1979. Reproductive costs in the house martin *Delichon urbica*. *J. Anim. Ecol.* 48:655-675.

Clobert J., Lebreton J.D., Clobert-Gillet M. and Coquillart H. 1985. The estimation of survival in bird population by recaptures or sightings of marked individuals. (Pp. 197-213). In: *Statistics in Ornithology*. Springer-Verlag, Berlin.

Clutton-Brock T.H. 1988. Reproductive success. *The University of Chicago Press*, Chicago.

Cody M.L. 1966. A general theory of clutch size. *Evolution* 20:174-184.

Cormack R.M., 1964. Estimates of survival from the sigthing of marked animals. *Biometrika* 51:429-438.

Coulson J. C. and Thomas C. 1985. Differences in the breeding performance of individual kittiwake gulls, *Rissa tridactyla* (L.). In: (Sibly R.M. and Smith R.H., eds.) *Behavioural Ecology; ecological consequences of adaptive behaviour*, pp. 489-503 Blackwell Scientific Publications, Oxford.

Cramp S. (ed.) 1985. The birds of the Western Palearctic. *Vol. IV. Oxford Univ. Press, Oxford.*

Cucco M., Malacarne G., Orecchia G. and Boano G. 1992. Influence of weather conditions on pallid swift *Apus pallidus* breeding success. *Ecography* 15:184-189.

Dobson A.P. 1983. Survival rates and their relationship to life-history traits in some common British bird. Pp. 115-146. In: (Power D.M., ed.) *Current Ornithology*, Vol. VII, Plenum Press.

Dobson A.P. 1987. A comparison of seasonal and annual mortality for both sexes of fifteen species of common British birds. *Ornis Scandinavica* 18:122-128

Dunnett G. M. and Ollason J.C. 1978. The estimation of survival rate in the Fulmar *Fulmarus glacialis* . *J. Anim. Ecol.* 47:507-520.

Finlayson J.F. 1979. The ecology and behaviour of closely related species in Gibraltar with special reference to swifts and warblers. *Unpublished Ph.D. Thesis, Oxford University.*

Fisher J. 1975. The relationship between deferred breeding and mortality in the Laysan albatross. *Auk* 92:433-441.

Fowler J. and Cohen L. 1992. Statistics for ornithologists. BTO Guide n. 22, *British Trust for Onithology*, Tring.

Glutz von Blotzheim U.N. and Bauer K.M. 1980. Handbuch der Vogel Mitteleuropas. *Aula Verlag, Wiesbaden.*

Haldane J.B.S. 1955. The calculation of mortality rates from ringing data. *Acta XI Congr. int. Orn.*, Basel, pp.454-458.

Jolly G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225-247.

Johnson H.D., Burnham K.P. and Nichols J.D. 1986. The role of heterogeneity in animal population dynamics. *Proc. International Biometrics Conf.* 13, 15 pp.

Koskimies J. 1950. The life of the Swift *Micropus a. apus* L. in relation to the weather. *Ann. Acad. Scient. Fenn.* 4:5-151.

Lack D. 1954. The natural regulation of animal numbers. *Oxford Univ. Press*, Oxford.

Lack D. 1956. Swifts in a tower. *Methuen and C., London.*

Lack D. 1966. Population studies of birds. *Oxford Univ. Press, Oxford.*

Malacarne G. and Griffa M. 1987. A refinement of Lack's method for swift studies. *Sitta* 1:175-177.

Malacarne G., Cucco M. and Orecchia G. 1992. Nest attendance, parental roles and breeding success in the Pallid Swift (*Apus pallidus*). *Vogelwarte* 36:203-210.

Mennella C. 1967. Il clima d'Italia nelle sue caratteristiche e varieta' e quale fattore dinamico del paesaggio. *Edart, Napoli.*

Newton I. 1989. Lifetime reproduction in birds. *Academic Press, London.*

Nichols J.D., Noon B.R., Stokes S.L. and Hines J.E. 1981. Remarks on the use of mark-recapture methodology in estimating avian population size. *Study in Avian Biology* 6:121-136.

Nichols J.D. and Pollock K.H., 1983. Estimation methodology in contemporary small mammal capture-recapture studies. *J. Mammal.* 64:253-260.

Perrins C.M. 1971. Age of first breeding and adult survival rates in the swift. *Bird Study* 61-70.

Perrins C.M. 1970. The timing of birds' breeding seasons. *Ibis* 112: 242-255.

Pianka E.R. 1970. On r- and k-selection. *American Naturalist* 104:592-597.

Pollock K.H., Nichols J.D., Brownie C. and Hines J.E. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 54:1-97.

Seber G.A.F. 1965. A note on the multiple-recapture census. *Biometrika* 52:249-259.

Seber G.A.F. 1982. The estimation of animal abundance and related parameters. *Second ed., Griffin, London.*

Weitnauer E. 1947. Am neste des Mauerseglers *Apus apus. Orn. Beob.* 44:133-182.

Weitnauer E. 1980. Mein vogel. *Basellandschaftlicher Natur- und Vogel Schutzverband Verlag, Liestal.*

Wooler R.D., Bradley J.S., Skira I.J. and Serventy D.L. 1989. Short-tailed Shearwater. In: Newton I. Ed. Life time reproduction in birds. *Academic Press, London* pp. 405-417

Yeatman L. 1976. Atlas des Oiseaux nicheurs de France de 1970 a 1975. *Societé Ornithologique de France, Paris.*

Avocetta N° 17: 199-202 (1993)

Long term changes in weather and in the breeding schedule of Common Swifts *Apus apus*

DAVID L. THOMPSON[(1)] and THE LATE HENRY DOUGLAS HOME.

(1) Applied Ornithology Unit, Zoology Department, Glasgow University - Glasgow G128QQ Scotland

Abstract At a small colony in Southern Scotland, long term changes in weather, have been associated with correponding changes in the date at which the chicks of Common swifts *Apus apus*, have reached the later stages of development. The dates at which the young have reached a suitable stage for ringing, have been significantly influenced by rainfall and temperatures in May and June. All of these variables have shown regular changes through time. There is also some evidence that July temperatures may also have changed through time and had additional effects. While the strong effects of weather in the early part of the season are consistent with there being effects of laying date and incubation period on changes in the breeding schedule, the changes in June and July weather during the later stages of breeding, may have had effects on chick growth rates which are known to be highly flexible in this species.

Introduction

In addition to the effects of environmental conditions on laying date (e.g. Perrin and Birkhead 1983, Cucco *et al.* 1992, Gory 1987) and incubation period, swifts are subject to strong environmental influences on chick growth rate (Lack and Lack 1951, Thibault *et al.* 1987). They may thus be expected to show considerable variance in fledging date depending on annual weather conditions. Weather around a small colony of swift in the Eastern Scottish Borders has shown long term changes over the period 1954 to 1992, and these have had significant effects on the breeding performance of the birds (Thomson and Douglas-Home in prep.). Using data collected on these swifts over this period (Douglas-Home 1977), we examine the prediction that the breeding schedule is variable and has been altered by changes in the weather, and we resolve where possible the effects of weather during the three months of the breeding season in order to identify at which breeding stage the effects upon breeding chronology are most marked.

Methods

In 1954, nest boxes for swifts were erected beneath the windows of a large country house, the 'Hirsel' near Kelso in the Borders of Scotland. These proved successful, and the number of boxes was increased quickly to a final total of 15. The data cover a total of 37 years, and over 220 breeding attempts. In only 1963 and 1964 were records not collected. During single visits in July of each year, it has been possible to ring adults and young, and note the productivity of each nest. Using observations of the birds before the selected date, as well as the habits and impressions established in the preceding 1 or 2 years, it was possible to time the visit to coincide with the presence of large feathered young of suitable age for ringing. Throughout this paper 'date' refers to the time of this visit. Clearly, though most chicks were large, feathered and close to fledging, this developmental stage is somewhat arbitrary, and is not equivalent to fledging date or laying date. Despite the statistical noise which may be generated by this, no confounding biases can be identified. Standard measures of temperature and rainfall are available locally from 'Floors Castle', Kelso, and cover the entire period. Sunshine and wind speed records have not been collected at this station. Long term trends in these weather patterns have been identified, and have been found to have significant effects on the breeding productivity of the birds in the colony (Thompson and Douglas-Home in prep.). These weather changes are thought to be a local rather than a widespread phenomenon (R. Tabony, Meteorological Office, Pers. comm.). To contend with noise around the long term trends, and to acknowledge the inevitable effects of date in year 'n' upon the date chosen in year 'n+1', running means over periods of 3 years were calculated (c.f. Aebischer *et al.* 1990, Digby *et al.* 1989). Although sine functions were fitted, the duration of the study was not long enough, to use stan-

---

Accepted 29 April, 1993

dard time series approaches such as 'ARIMA' to investigate whether the patterns were genuinely cyclical. As well as fitting functions to model each variable in time, multiple regression was used to examine and separate the effects of several weather variables on ringing date (Lane *et al.* 1987). The origin of the years was moved to 1953 to avoid computing errors associated with very large sums of squares. Where multiple linear regression was used, variables were added into the model in various orders, and full models were constructed using all variables which had at least one significant effect. The significance of these variables was then tested by examining the change in explained variance, when each was dropped from the full model. The significance of other variables was tested by examining the changes when they were added to the full model.

Results

Graphs of 3-year running means for July chickringing date, and the number of days with rainfall in excess of 1 mm during the months of May and June, are given in Figure 1. Trends in mean daily maximum temperatu-res for the months May, June, and July are given in Figure 2. Multiple regression (Lane *et al.* 1987, Digby *et al.* 1989) was used to compare the fit of sine or quadratic functions with that of simple linear fun-ctions. The results of fitting these functions are given in Table 1. A multiple linear regression model was con-structed to examine all the effects of the weather vari-ables on ringing date. (see Table 2. for these results).

The model can be expressed as:

July date = -38.1-(1.422 x No. June days with rain fall >1mm)
+(3.67 x Mean daily max May temperature)
+(1.056 x No. May days with rainfall >1mm)
+(1.372 x Mean daily max June temperature)
-(1.112 x Mean daily max July temperature).

This accounts for 58.1% of the variance in running means of the date selected for ringing.

The ringing date has been later in years when there have been lower temperatures in May and June, lower May rainfall, higher June rainfall, and higher July temperatures. The signs of the May rainfall effect and the July temperature effect would seem counter intuitive, though the latter effect is weak.

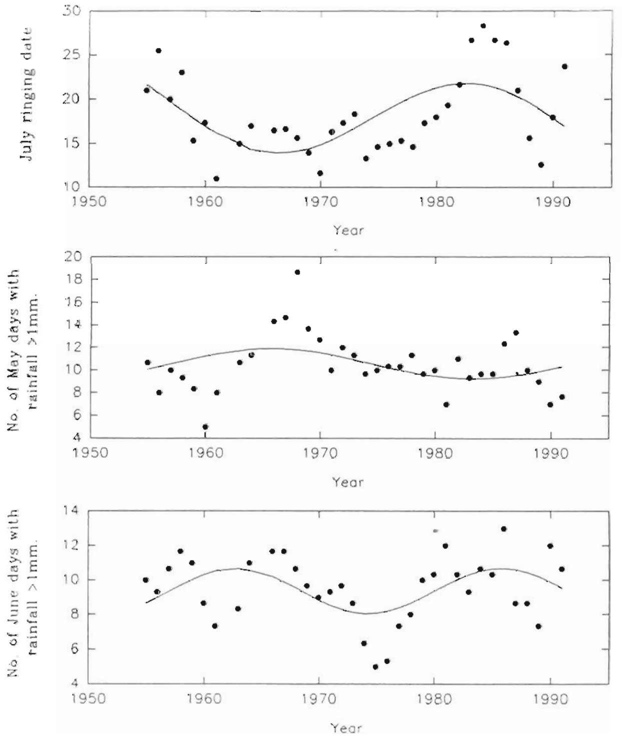


Figure 1.Graphs showing trends in the 3 year running means for the date at which chicks reached the large feathered stage, and the number of days in May and June with rainfall greater than 1mm. Lines show fitted sine functions.

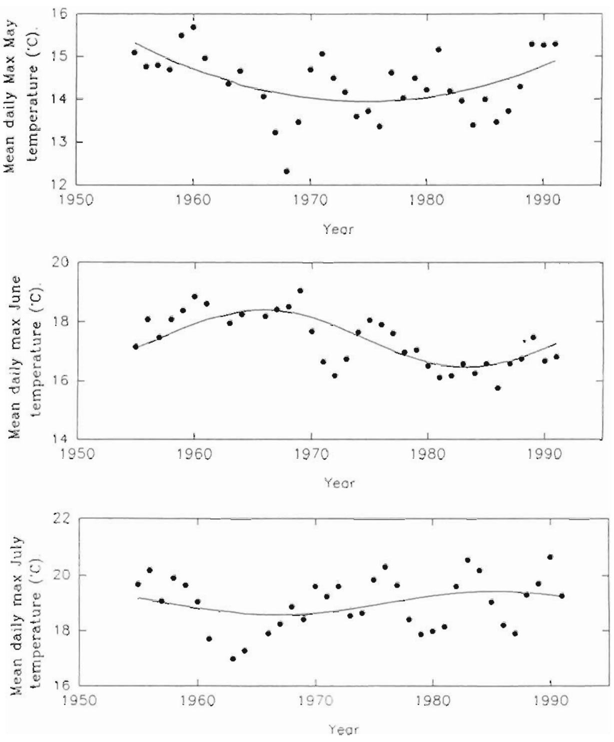


Figure 2. Graphs showing trends in the 3 year running means of mean daily maximum temperature during the months of May, June, and July. Lines show fitted quadratic or sine functions.

Table 1. Functions describing trends in weather and ringing date. All variables are 3-year running means.

Variable	Function type	Statistics.
July ringing date.	Sine	$F_{1,33}=14.451$, $P<0.01$, explained $S^2=28.4\%$.
No. May days, rain >1mm	Sine	$F_{1,33}=4.872$, $P<0.05$, expl. $S^2=10.2\%$.
No. June days, rain >1mm	Sine	$F_{1,33}=9.361$, $P<0.01$, expl. $S^2=19.7\%$.
Mean daily max May T.	Linear and quadratic	Linear: $F_{1,33}=9.178$, $P<0.01$ quadratic: $F_{1,33}=8.501$,$P<0.01$, explained $S^2=23.6\%$
Mean daily max June T.	Linear and sine	Linear: $F_{1,33}=4.472$,$P<0.05$ Sine: $F_{1,33}=9.297$,$P<0.01$ expl. $S^2=58.4\%$.
Mean daily max July T.	(Sine)	$F_{1,33}=3.785$,$P<0.1$, expl. $S^2=7.6\%$.

Table 2. Results from multiple linear regression models for the effects of weather variables on the date at which Common Swifts reached a suitable age for ringing. All variables are 3 year running means.

Variable dropped from full model.	Significance of change.
Mean daily maximum June temperature.	$F_{1,30}=4.375$, $P<0.05$.
Mean daily maximum May temperature	$F_{1,30}=8.504$, $P<0.01$.
Mean daily maximum July temperature	$F_{1,30}=3.517$, ($P<0.1$).
No. June days with rainfall >1mm.	$F_{1,30}=13.050$, $P<0.01$.
No. May days with rainfall >1mm.	$F_{1,30}=7.612$, $P<0.01$.
Variable added to full model.	
No. July days with rainfall >1mm.	$F_{1,28}=0.541$, N.S.

Discussion

The mechanisms behind the relationship found in this study may not be simple. At least four components of weather - temperature, sunshine, wind speed, and rainfall - have been found to be important for chick growth rates in Swifts (Lack and Lack 1951) and weather in the prelaying stage has been found to affect the laying date of Common and Pallid Swifts Apus pallidus (Cucco *et al.* 1992, Gory 1987, Thibault *et al.* 1987). No sunshine or wind speed records are available for this colony, but additional long term trends in breeding success, after controlling for temperature and rainfall, suggest that other features of the environment, such as sunshine, wind speed, or insect availability, may have changed in tandem with measured weather variables (Thomson and Douglas-Home in prep.) Thus although the meteorological variables for which data are available do show marked and significant associations with ringing date, it cannot necessarily be concluded that these variables have caused direct or independent changes in the breeding schedule. The patterns are however largely consistent with predictions from the species biology (Lack and Lack 1951). The mechanism may include a direct effect on feeding conditions and an indirect effect on the abundance of aerial insects (e. g. Bryant 1975). While low rainfall in May and higher temperatures in July may be directly detrimental to the birds, these associations with late ringing date may also be due to a more complex indirect relationship with other weather variables or insect abundance.

Since chicks were often ringed within the first two weeks of July, weather during the whole month would naturally be expected to have smaller effects than that during earlier months. The importance of May weather may have influenced laying and hatching dates, but the effects of weather during the later parts of the breeding season suggest that the considerable flexibility in growth rates may also be an important source of variance in the timing of fledging.

Acknowledgements - While the project was set up by H.D.-H, many of the data used in this analysis were collected by other naturalists and bird-ringers, including Mssrs W. Murray, A. MacMillan, S. da Prato, A. Kerr., C. Badenoch, and the late R.J. Robertson . C.O. Badenoch has provided help with the archiving and collating of records, and with attempts to obtain research grants. Lady Caroline Douglas Home has kindly allowed us access to the birds each years. Drs. P. Monaghan, and R.W. Furness have supervised DLT while analysing the data. The Carnegie Trust for the Universities of Scotland generously supported the analysis with a research grant. J. Currall, and J. Buchanan provided help and advice with statistics and computing. Staff at the Meteorological Office provided help with the provision of data and discussed long term trends. Dr. P. Monaghan kindly read and commented on an earlier draft of this manuscript.

Riassunto- In una piccola colonia di Rondone comune *Apus apus*, situata nel Sud della Scozia, si è evidenziata una relazione tra cambiamenti a lungo termine del tempo atmosferico e i corrispondenti cambiamenti della data di involo dei giovani nidiacei. Le date in cui i giovani hanno raggiunto uno stadio adatto per l'inanellamento sono state significativamente influenzate dalla piovosità e dalle temperature di maggio e giugno. Tutte queste variabili hanno presentato cambiamenti regolari nel tempo. Vi sono inoltre alcune evidenze che le temperature di luglio possono essere cambiate negli anni ed avere influenzato ulteriormente la riproduzione. Nella prima parte della stagione riproduttiva il clima ha influenzato fortemente la data di deposizione e il periodo di deposizione, mentre i cambiamenti climatici di giugno e luglio, che coincidono con gli studi finali dello sviluppo, possono avere avuto effetto sulla velocità di accrescimento dei piccoli.

References

Aebischer N.J., Coulson J.C. and Colebrook J.M. 1990. Parallel long-term trends across four marine trophic levels and weather. *Nature* 347:753-755.

Bryant D.M. 1975. Breeding biology of house martin *Delichon urbica* in relation to aerial insect abundance. *Ibis* 117:180-216.

Cucco M., Malacarne G., Orecchia G. and Boano G. 1992. Influence of weather conditions on pallid swift *Apus pallidus* breeding success. *Ecography* 15:184-189.

Digby P., Galwey N. and Lane P. 1989. Genstat 5. A Second Course. Oxford Science Publications. *Clarendon Press, Oxford.*

Douglas-Home H. 1977. The Birdman. Memories of birds. *Collins, London.*

Gory G. 1987. Influence du climat mediterraneen sur la reproduction du martinet noir (*Apus apus* L.). *Oiseau et Rev. Francais. Ornith.* 57:69-84.

Lack D. and Lack E. 1951. The breeding biology of the Swift *Apus apus. Ibis* 93:501-546.

Lane P., Galwey N. and Alvey N. 1987. Genstat 5. An Introduction. Oxford Science Publications. *Clarendon Press, Oxford.*

Perrins C.M. and Birkhead T.R. 1983. Avian Ecology. *Blackie, Chapman and Hall, New York.*

Thibault J.C., Brunstein D., Pasquet E. and Guyot I. 1987. La reproduction du martinet pale (*Apus pallidus*, Shelley) sur des ilot satellites de la Corse: ses relations avec les facteurs climatiques. *Rev. Ecol. (Terre Vie)* 42:277-296.

Avocetta N° 17: 203-207 (1993)

Nesting chronology, molt, and ectoparasites of Vaux's Swifts in northeastern Oregon

EVELYN L. BULL and CHARLES T. COLLINS

USDA Forest Service, Pacific Northwest Research Station- La Grande, OR 97850 U.S.A.
Dept. of Biology, California State University - Long Beach, CA 90840 U.S.A.

Abstract—We recorded nesting chronology at 15 Vaux's Swift (*Chaetura vauxi*) nests. Nest building was observed as early as 3 June. Nestlings were present from 2 July to 4-7 September and were in the nest at least 27-32 days. Molt of primaries began in early July and probably ended after the swifts left the area. Weight of 30 adults averaged 18.5 g. One species of feather louse and 1 species of feather mite were collected.

Introduction

Little information is available on the nesting chronology, molt, or ectoparasites of the Vaux's Swift (*Chaetura vauxi*) in North America. Three studies (Bent 1940, Baldwin and Hunter 1963, Baldwin and Zaczkowski 1963) have reported dates on the nesting chronology of these swifts. This study provides additional information in a different area.

These swifts are difficult to find nesting in forests and even more difficult to catch while nesting to measure characteristics such as molt and weight. This basic information on life history is essential to understanding the ecology of the species. Our objectives were to record nesting chronology, patterns of molt, ectoparasites, and weights of Vaux's Swifts during the nesting season.

Methods

We searched for nest trees used by Vaux's Swifts in 4 study areas in June and July 1992. The areas (Syrup, Frog Heaven, Ukiah, and Balm) are primarily mixed coniferous forests and were selected on the basis of observed swift abundance. Syrup and Frog Heaven are 35 km west-southwest and 41 km southwest of La Grande, Union County, Oregon, respectively. The Ukiah area is 17 km west of Ukiah, Umatilla County, Oregon. Balm is 38 km southeast of Union, Baker County, Oregon.

To locate nests, we spent 1 hour watching hollow trees that swifts had used previously for nesting (Bull and Cooper 1991) and by watching additional hollow trees suitable for nesting in the 4 areas. Swifts flying in or out of a tree during the day indicated that the tree was being used for nesting.

We gathered information to determine nesting status by recording activity for about 9 hours (approximately 09:30-18:30) at 2 nests during nest building and at 3 nests during the incubation and nestling stages. We recorded behavior and the time swifts entered or left the nest tree. We calculated frequency of visits to the nest by determining the minutes between times that swifts entered the cavity. Time in the nest was the interval between when a swift flew into the cavity and when a swift flew out. From these 9-hour observations, we were able to ascertain the status at other nests in about an hour each week, based on the time the swift was in the nest and the interval between visits.

Molt and weight were recorded for adults that were trapped in mist nets suspended in front of nest cavities. Trapping was not done during incubation to reduce the risk of abandonment. We attempted to catch swifts every 2 weeks for measurements; however, the birds frequently escaped from the net. Most birds were captured once, about half were captured twice, and a few were captured 3 and 4 times.

Captured birds were lowered to the ground and removed from the net. We measured the right wing chord and weight and recorded presence of parasites and molt of the primaries and rectrices. Parasites were collected and preserved in alcohol. Each time we caught a bird we weighed it; the weight reported for a particular bird is the average of its weights.

Accepted 21 March, 1993

We measured the total length of each new primary and the portion out of the sheath. For the first 10 birds, we measured molt on both wings; however, molt was always the same for each wing, so only measurements for the right wing were recorded thereafter. For the analysis, we calculated the state of molt of individual primaries by using the following categories and scores (Newton 1966):

Old feather	0
Feather missing or in small pin stage	1
Feather in large pin or brush stage	2
Feather brush to half grown	3
Feather half to three-quarters grown	4
Feather three-quarters to full length	5

To determine the score, we divided the length of the partially grown feathers by the length of that feather fully grown (measured from birds with fully molted feathers). We used the following lengths for fully molted feathers: 36 mm for primary 1, 42 mm for 2, 49 mm for 3, 57 mm for 4, and 64 mm for 5. There was a potential score of 50 for each wing if the molt was complete and thus a total potential score of 100 for each bird. In the birds captured primaries 7-10 had not molted, and no complete molt of primary 6 was observed. A linear regression of primary molt score on julian date was computed to determine rate of growth and the start and end of molt.

Rectrices were measured and scored in the same fashion as primaries. If molt was complete, the score was 50. Only 6 birds with rectrices molting were captured, so no analysis was done.

Results

Nesting chronology

Nesting chronology was recorded for 15 nests and will be discussed in 3 stages: nest building, incubation, and nestling. We observed nest building behavior from 3 June to 23 June (Fig. 1). During nest building, swifts broke small twigs off trees while flying through the branches. After several passes through a tree, the swift entered the nest tree and remained inside for a mean of 17 (nest B) and 24 minutes (nest A) (Table 1). We presumed that the bird was positioning the sticks in the nest with saliva. The interval between visits to the nest tree averaged 79 and 42 minutes for the 2 nests watched (Table 1).

We observed incubating birds as early as 18 June and as late as 25 July (Fig. 1). The interval between visits to the nest averaged 38, 53, and 55 minutes for 3 days of observation (Table 1). There was considerable variation in the amount of time a bird was in the nest tree. The average time for nest C (Table 1, first entry) was 2 minutes for the first 7 nest visits, but then 2 birds stayed in for 37 and 69 minutes. On the second day of observation at nest C (Table 1, second entry), the average time in the nest was 2 minutes. Nest B did not reflect this short time exchange, because 3 birds entered the nest tree, and some of them remained in the cavity.

Table 1 - Interval between visits to the nest and time spent in the nest tree during nest building, incubation, and when nestlings were present at 4 Vaux's Swift nests. Each line represents 9 hours of observation (approximately 09:30- 18:30) at each nest, northeastern Oregon, 1992.

		Interval between visits to nest (min)		Time in nest (min)	
Nest	Activity	Mean	Range	Mean	Range
A	Nest building	79	3-155	24	4-41
B	Nest building	42	5-70	17	4-27
B	Incubation	38	8-89	37	11-78
C	Incubation	55	17-100	14	1-69
C	Incubation	53	25-77	2	1-4
B	Nestlings	20	1-44	1	1-7
C	Nestlings	17	1-40	12	1-41
D	Nestlings	13	5-64	7	1-65

Nestlings were present from 2 July to 4-7 September (Fig. 1). The time the young were in the nest tree was > 30-32 days at 3 nests, > 28 days at 2 nests, and 27-29 days at 1 nest. The adults returned to the nest an average of every 13, 17, and 20 minutes at 3 nests and remained in the nest an average of 1, 7, and 12 minutes (Table 1). For the 3 nests, there was an average of 3.6 visits/hour to feed young. The 3 nests where we recorded activity throughout the day had young < 15 days old.

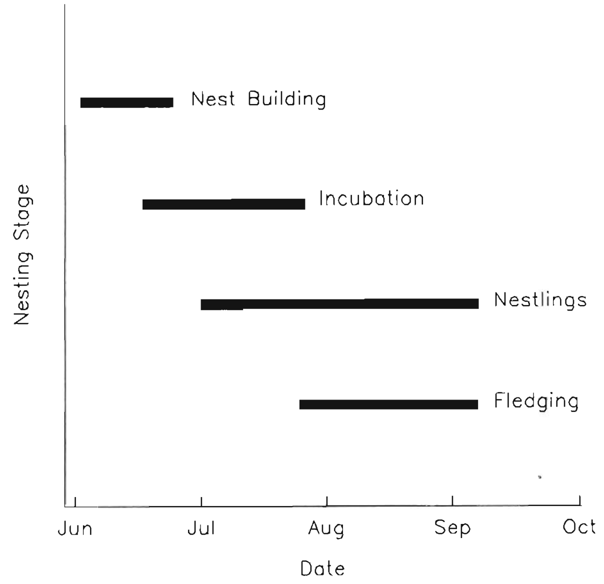


Figure 1 - Nesting chronology at Vaux's Swift nests in northeastern Oregon, 1992.

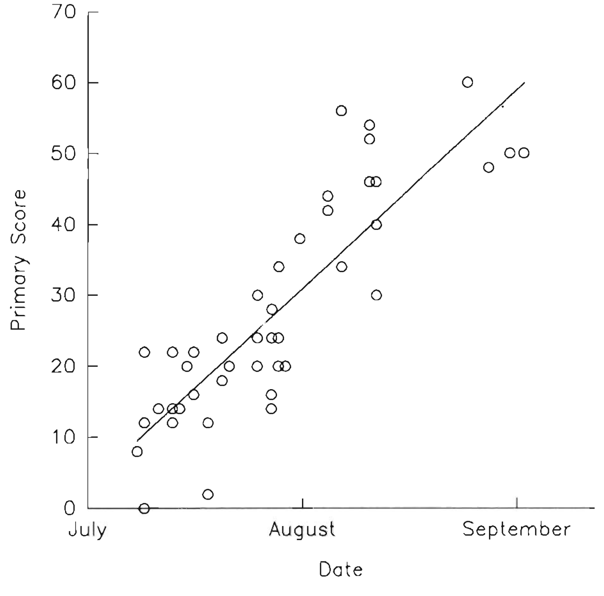


Figure 2 - Molt score of primaries in relation to date for 30 swifts captured a total of 47 times in northeastern Oregon, 1992. Primary score is for both wings.

The earliest date that young fledged was 26 July, and the latest was between 4 and 7 September. The mean fledging date of 10 nests at 9 nest trees (1 tree had 2 nests) was 7 August. Of the 15 nest trees observed, 9 had young fledge, 1 failed during nest building or incubation, 2 failed with nestlings, and in 3 the results were unknown.

Primary molt

We caught 30 adults (12 of them more than once) and recorded a total of 47 molt measurements (Fig. 2). Birds were first captured on 9 July, when primary molt had just begun. Molt of the primaries progressed from the proximate to distal. The last bird was captured 1 September and had an arrested molt ending with the sixth primary. The linear regression of primary score (y) on date (x) was:

$$y = -164.52 - 0.92x.$$

Setting $y = 0$ (no molt occurring yet) suggests that molt started 27 June, so most swifts started molting primaries shortly after their eggs hatched (Fig. 1). Setting $y = 100$ (molt complete) suggests that molt ended 14 October, which means that molt took 109 days to complete. This period could be somewhat longer if the growth rate of the longer primaries, 7-10, was slower than the growth rate of the shorter primaries, 1-6 (Fig. 3).

We observed a roost in the Ukiah study area each week from 4 August until 25 September. During the first 2 weeks in September, > 500 swifts went in the roost. On 16 September, only 283 swifts went in. On

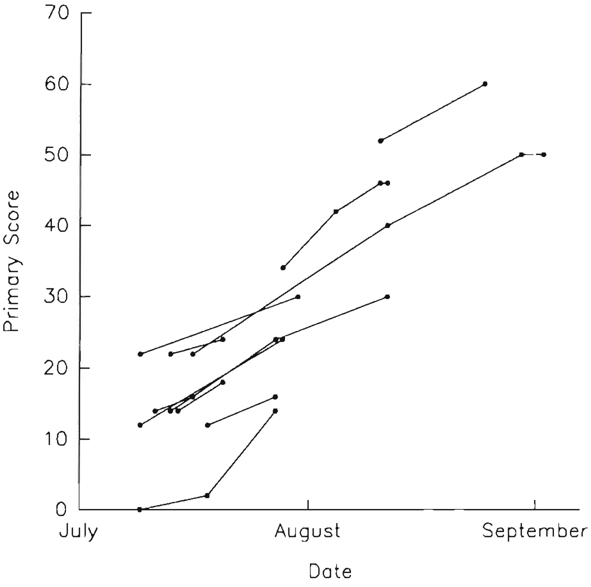


Figure 3 - Rate of increase in primary score (both wings) in relation to date in adult nesting swifts in northeastern Oregon, 1992. Each line refers to a particular individual, and its slope indicates the rate of molt in the primary feathers in points per day.

20 September, 102 swifts went in, and the next night only 12 went in. So it appears that the swifts migrate before the molt is complete

Rectrix molt

Only 6 swifts of those captured were molting rectrices; the earliest capture was 31 July and the latest was 27 August. Ten swifts caught during this period were not molting rectrices. The rectrices were replaced from the outermost inward, and molt scores ranged from 8 to 34 (potential of 50 with all new rectrices). All 6 swifts retained 2-5 old rectrices, and rectrices 1-2, 1-3, or 1-4 were growing in. Molt of these rectrices occurred when primaries 4 and 5 or when 5 and 6 were coming in. Two birds had asymmetrical molt with the third or fourth rectrix missing on 1 side.

Measurements

We captured 30 adult and 6 juvenile swifts. The average weight of adults was 18.5 g (SD = 1.16, range = 15.5-22.2), and for juveniles it was 17.6 g (SD = 1.0, range = 16.6-19.1). The average wing chord length was 113.6 mm (SD = 2.70, range = 109-118) for adults and 111.5 mm (SD = 5.32, range = 105-118) for juveniles.

Ectoparasites

We first discovered feather louse (Mallophaga) eggs on the feathers of the nape of a swift on 28 July. All 16 adult swifts captured after that date had eggs or lice on them; 3 of 6 juveniles had eggs or lice. The ectoparasites collected were 1 species of feather louse (*Dennyus dubius*) and 1 species of feather mite (*Berlesella* sp.); this mite probably represents a new species as we know of no previous reference to *Berlesella* in North America (N. A. Wilson, Univ. of Northern Iowa, Cedar Falls; pers. comm.). *Dennyus dubius* has been reported previously on the Chimney Swift (*Chaetura pelagica*) and *D. vauxi* on the Vaux's Swift (Emerson and Pratt 1956).

Discussion

The nesting chronology we observed was fairly consistent with the dates reported in the literature. Baldwin and Zaczkowski (1963), Baldwin and Hunter (1963), and Bent (1940) report that eggs hatched on 10 July, 14 July, and in "early July," respectively. Ten of the 15 nests we observed had eggs hatch in late June and early July. In Montana (Baldwin and Zaczkowski 1963, Baldwin and Hunter 1963), young left the nest tree 28-30 days after hatching (7-9 August); the birds we observed left the nest tree > 28-32 days after hatching. Ten of the nests we observed had young leave between 26 July and 10 August, while young left the last nest between 4 and 7 September. We think this late nest was a renesting attempt, because swifts first were observed incubating in this tree on 24 June. Even though swifts were entering the tree in June and July, feeding of nestlings was not observed until 4 August.

Molt of primaries and rectrices was variable in our study areas (Fig. 2). Baldwin and Hunter (1963) noted a similar variability in Montana where in 1961 2 swifts had not started to molt primaries by 27 July, and 2 others had molted the first 3 and first 5 primaries by 4 and 11 August, respectively. In 1962, 4 swifts were molting primaries 2-6 on 9 August (Baldwin and Zaczkowski 1963).

The molt probably was not completed before the swifts migrated; however, some swifts in the Ukiah study area spent part of each day in a communal roost in August and September after young left the nest. The swifts entered the roost shortly before dark but some did not leave the roost until after 10:30 in September. We suspect they were building their body reserves for migration and progressing with their molt during this time. Bent (1940) reports that swifts started roosting in a chimney in Washington in mid-August and in 10 days > 500 were roosting there; over the next 16 days, their numbers gradually declined to only 3 swifts roosting in the chimney.

The overlap of breeding and molting has been recorded in other swifts (Kainady 1977, Cramp 1985) and particularly in *Chaetura* (Fischer 1958, Collins 1968). Arrested molt also has been described, particularly in migratory species (Cramp 1985). The migratory Chimney Swift of Eastern North America appears to complete its primary molt by early October while still in the early stages of migration (Coffey 1958).

Vaux's Swifts in Montana had a mean weight of 17.2 g (N = 4, range = 16.4-19.0) in late July (Baldwin and Hunter 1963) and 19.2 g (N = 5, range = 18.3-19.9) in early August (Baldwin and Zaczkowski 1963). Two samples of spring migrant Vaux's Swifts in California averaged 15.4 g (N = 35, range = 14.1-17.4; Collins 1971) and 17.1 g (N = 72, range = 15.0-20.9; Collins unpubl. data). These data generally are similar to those presented here and do not reflect the dramatic increase in body weight (51%) of fall migrants reported for *C. pelagica* (Coffey 1958).

All the adult swifts captured had either feather lice or eggs of feather lice. One recently fledged juvenile had > 30 eggs and > 6 adult lice and was in poor condition. Watson (1933) reports Vaux's Swifts heavily parasitized by lice and weak and emaciated during migration in California. Possibly a heavy infestation of biting lice can jeopardize survival of swifts, particularly if the birds are energetically stressed, as during migration.

The swifts displayed considerable variability in nesting chronology because of the 41-day difference between when the first and last nest had young leave. The swifts appeared to be synchronized in the time (16-21 September) they left the Ukiah study area, however. Time of nesting, parasite loads, stage of molt, and weights of swifts when they leave the breeding grounds no doubt have a great deal to do with their survival during migration.

Acknowledgments - We thank B. E. Carter, H. D. Cooper, R. Guse, J. E. Hohmann, C. Hunter, K. I. Kronner, P. E. Talbot, B. C. Wales, and B. R. Younker for their assistance with field work. N. A.Wilson identified the ectoparasites. Funding was provided by the USDA Forest Service, Pacific Northwest Research Station.

Riassunto - Si è osservata la cronologia di nidificazione in 15 nidi di *Chaetura vauxi.* La prima nidificazione data 3 giugno. I nidiacei sono stati visti al nido dal 2 luglio al 4-7 settembre e permangono nel nido almeno 27-32 giorni. La muta delle primarie è iniziata ai primi di luglio e probabilmente è terminata dopo che i rondoni hanno abbandonato l'area di nidificazione . Il peso di 30 adulti è in media 18.5 g. Sí sono raccolti una specie di pidocchio ed una di acaro delle penne.

References

Baldwin, P. H., and W. F. Hunter. 1963. Nesting and nest visitors of the Vaux's Swift in Montana. *Auk* 80:81-85.

Baldwin, P. H., and N. K. Zaczkowski. 1963. Breeding biology of the Vaux's Swift. *Condor* 65:400-406.

Bent, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies. Part II. *Bull. U.S. Natl. Mus.* 176.

Bull, E. L., and H. D. Cooper. 1991. Vaux's Swift nests in hollow trees. *Western Birds* 22:85-91.

Coffey, L. C. 1958. Weights of some Chimney Swifts at Memphis. *Bird-Banding* 29:98-104.

Collins, C. T. 1968. The comparative biology of two species of swifts in Trinidad, West Indies. *Bull. Florida State Museum* 11:257-320.

Collins, C. T. 1971. A probable swift-cactus collision. *Calif. Birds* 2:101.

Cramp, S., ed. 1985. The birds of the western Palaearctic. *Vol. 4. Oxford Univ. Press.* 960 pp.

Emerson, K. C., and H. D. Pratt. 1956. The menoponidae (Mallophaga) found on North American swifts. *Jour. Kansas Ent. Soc.* 29:21-28.

Fischer, R. B. 1958. The breeding biology of the Chimney Swift *Chaetura pelagica* (Linnaeus). *N. Y. State Museum and Sci. Service. Bull.* 368:1-141.

Kainady, P. V. G. 1977. The overlap of breeding and moulting in some Iraqi birds. *Bull. Basrah Nat. Hist. Mus.* 4:65-68.

Newton, I. 1966. The moult of the Bullfinch *Pyrrhula pyrrhula. Ibis* 108:41-67.

Watson, S. A. 1933. The Vaux Swift at Whittier, California. *Condor* 35:203-204.

Avocetta N 17: 209-210 (1993)

Toe atrophy caused by carpenter ants in Vaux's Swifts

EVELYN L. BULL and TOROLF R. TORGERSEN

USDA Forest Service, Pacific Northwest Research Station, La Grande, OR 97850 USA

Abstract - Three cases of toe atrophy caused by carpenter ants *Camponotus* sp. are described in Vaux's Swift in northeastern Oregon. We monitored 11 Vaux's Swift (*Chaetura vauxi*) nests in 1993 in Union, Umatilla, and Baker Counties in northeastern Oregon, USA.

We monitored 11 Vaux's Swift *(Chaetura vauxi)* nests in 1993 in Union, Umatilla, and Baker Counties in northeastern Oregon, USA.

These nests were in hollow grand fir *(Abies grandis)* trees in mixed conifer stands (Bull and Cooper 1991). We trapped 21 adults at these nest trees in July. We also trapped 161 swifts at communal roosts in the same areas in August.

Two adults and 2 juveniles had 1 or 2 carpenter ants (*Camponotus* prob. *modoc* Wheeler) clinging to their toes (Fig. 1). When the swifts were captured, all that remained of the ants was the head attached to the toe by the locked mandibles. One toe on an adult and 2 toes on a juvenile, both with ant heads attached, had atrophied and were no longer functional. The toes on the other 2 swifts were swollen and inflamed from the bite but still apparently functional.

We suspect there were colonies of ants in the nest trees (Sanders 1964), and that the swifts were bitten while they were incubating or roosting in the trees. At the time the affected Bull and Torgersen adults were captured, excavating dust or large ants were observed on the boles of these nest trees. Ants may have been foraging or on foraging trails inside the tree when they encountered the swifts. Ants are common predators of other arthropods, or scavengers of dead or disabled arthropods and small vertebrates (Ayre 1963, Borror and DeLong 1971, Torgersen *et al.* 1990). In 1990 we observed a carpenter ant colony in a tree that housed a swift nest. When we cut a hole in the side of the tree to observe the nest which was 6 m above the ground, hundreds of carpenter ants swarmed out of the tree wall.

Once bitten, the swifts probably pulled off as much of the ant as possible, leaving the mandibles and head attached. The bites appeared to have become infected, and with circulation impaired, the affected toes atrophied.

The 2 affected adults were captured during incubation at 2 different nests, and their nesting attempts failed. These were the only 2 failed nests of the 11 we monitored, including others where adults were captured. None of the adults at the other nests had

Figure 1. Head of a carpenter ant attached by its locked mandibles to the toe of a Vaux's Swift in northeastern Oregon, 1993.

Accepted 15 November, 1993

ants on their feet or showed evidence of ant attack. We suspect disturbance on adults or possibly attacks on nestlings by ants contributed to these nest failures.

Other authors have observed nest failures which provide circumstantial evidence that carpenter ants (*Camponotus* spp.) may have been involved. Conner and Lucid (1976) described nest failures of the European Starling (*Sturnus vulgaris*) and Eastern Phoebe (*Sayornis phoebe*), that they ascribed to possible predation or disturbance by carpenter ants. However, they also observed apparent coexistence of nestling Northern Flickers (*Colaptes auratus*) and a colony of carpenter ants in the same tree. Kilham (1971) speculated that a pair of Yellow-bellied Sapsuckers (*Sphyrapicus varius*) may have been forced to abandon a nest and their young because of disturbance by carpenter ants (*C. pennsylvanicus*) .

The incidence of ants we observed on nesting adults was quite high (10%), while the incidence on communally roosting birds was much lower (1%). This difference may be a function of the ability of roosting birds to readily move about within a roost or to a new roost tree. If ants attack early in the nesting cycle, the swifts could attempt to relocate. Whereas, if ants become a problem after a nest is in use, the consequences of a move would be abandonment of a clutch of eggs or of the nestlings. Typically, Vaux's Swifts in Oregon raise only 1 brood per year, so they would be unlikely to attempt to nest again.

Ramifications of the presence of ants in nest trees could include disabling injury or death of either nestlings or adults. If bitten by enough ants, the swifts would be unable to perch and would perish. Our data suggest that ants may affect the fitness of adults and directly or indirectly influence nesting success. Further, colonies in potential nest trees could limit the number of available nest sites, a resource already thought to be in short supply.

Riassunto - Si descrivono tre casi di atrofia delle dita di *Chaetura vauxi* causata dall'attacco di formiche del genere *Camponotus*.

References

Ayre G. L. 1963. Laboratory studies on the feeding habits of seven species of ants. *Can. Entomol.* 95:712-715.

Borror D. J. and DeLong D. M. 1971. An introduction to the study of insects. *Holt, Rinehart and Winston. New York.* 812 pp.

Bull E. L. and Cooper H. D. 1991. Vaux's Swift nests in hollow trees. *Western Birds* 22:85-91.

Conner R. N. and Lucid. V. J. 1976. Interactions between nesting birds and carpenter ants. *Bird-banding* 47:161-162.

Kilham L. 1971. Reproductive behavior of Yellow-bellied Sapsuckers. 1. Preference for nesting in *Fomes*-infected aspen and nest hole interrelations with flying squirrels, raccoons, and other animals. *Wils. Bull.* 83:159-171.

Sanders C. J. 1964. The biology of carpenter ants in New Brunswick. *Can. Entomol.* 96:894-909.

Torgersen T. R., Mason R. R. and Campbell R. W. 1990. Predation by birds and ants on two forest insect pests in the Pacific Northwest. *In*: Studies in Avian Biology No. 13:14-19. Avian foraging: Theory, methodology, and applications. *Eds.* M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr.

Avocetta N° 17: 211-212 (1993)

Newsletter

An international swift workshop at Galeria, Corse

For the first time to our knowledge, an international conference was entirely devoted to the swifts. From the 8th to the 11th of March 1994, 23 swift workers met under the auspices of the Parc Naturel Régional de la Corse. This workshop was organised by V. Bretagnolle, G. Gory and J.-C. Thibault, and was held at the Casa Marina in the Réserve Naturelle de Scandola, a new house (actually, the participants of the workshop baptised the Casa Marina!) owned by the Parc and used for hosting field courses and seminars. Michel Leenhardt (Directeur du Parc) opened the meeting, François Giacobbi (Président du Parc, Sénateur de Haute Corse) gave the welcoming address; and several journalists covered the meeting for local newspapers.

Partecipants came from the US (C. Collins), United Kingdom (D. Bryant, P. Lee, T. Martins), Switzerland (A. Engeler, D. Pfluger, H. Schmidt), Italy (G. Boano, M. Cucco, G. Malacarne), Spain (J.D. Rodriguez teilero) and France (V. Bretagnolle, D. Brunstein, G. Gory, J.-C. Thibault).

The talks covered systematics, aerial feeding, evolution, life history strategy (cost of reproduction, ectoparasites, breeding success), population dynamics, monitoring and conservation. All communications were of a very high standard, according to the partecipants, and revealed that swifts (at least for the three European species) ranked definitely amongst the most studied bird species.

Apart from oral communications, round tables were also organised; areas for future research were explored, and subjects such as sexual selection, feeding ecology, and host-parasite interactions were identified as the topics most in need of further research. Possible collaborative studies were also explored.

Another round table saw the birth of a Newsletter, "Swift Network", for which C. Collins is the first editor. The problems that urban nesting swifts face during restoration of old buildings and bridges were noted several times, and better cooperation among Europeans on this issue was called for: a first concrete action should be the publication for the International Ornithological Congress at Vienna of a leaflet descibing the several techniques that have been developed for such problems in Switwerland and France.

A field excursion ended the meeting: a tour at sea which permitted very good sightings by every-body of several rare species (osprey, audouin's gull, peregrine falcon, puffins, shearwaters, dolphins etc.).

The three organizers wish to express their gratitude to all participants for giving such enthusiasm and high standard to the meeting, and thank the Parc Naturel de la Corse for funding the workshop, the personnel of the Casa Marina for their excellente service, and the staff of the Réserve Naturelle de Scandola for the field trip.

Vincent Bretagnolle
CEBC-CNRS
Beauvoir sur Niort,
79360 France

Gérard Gory
13 bis Avenue Amiral Courbet
Muséum d'Histoire Naturelle
30000 Nîmes France

Jean-Claude Thibault
Parc Naturel Régional
BP417, 20184
Ajaccio Cedex, France

Participants of the Swift workshop at Galeria. From left to right. Back row: M. Cucco, C. T. Collins, A. Engeler, H. Schmid, Mrs. Engeler, D. Rodriguez-Teijero, two host organizers; front row: D. Brunstein, A. Penloup, T. Martins, J. C. Thibault, D. Bryant, V. Bretagnolle, G. Gory, two host organizers; crouched: P. Lee, D. Vinyoles, G. Malacarne, D. Pfluger, G. Boano.

Avocetta N° 17: 213-215 (1993)

Notices

Segnalazioni per la rubrica "Nuovi avvistamenti"

Cari amici,

dopo una pausa, che definire di riflessione potrebbe essere considerato eufemistico, la Direzione del C.I.S.O. e gli Editors di Avocetta hanno deciso di ridare vita e spazio alla rubrica **Nuovi avvistamenti**.

Le segnalazioni verranno pubblicate con un breve titolo ed a firma dei segnalatori (cfr. *Avocetta* 1989, 13:141-143). Le segnalazioni che necessitano di omologazione saranno automaticamente sottoposte al vaglio del Comitato di Omologazione Italiano (C.O.I.).

Questa rubrica ha la presunzione di proporsi vari obiettivi:

1) evitare che molti dati interessanti ammuffiscano nei cassetti delle scrivanie;

2) raccogliere in un'unica sede un'ampia massa di dati di rilevanza nazionale che, da soli, probabilmente non verrebbero pubblicati o verrebbero proposti a periodici locali, aumentando la difficoltà del loro reperimento bibliografico;

3) conglobare in una sola sede dati che possono acquisire significato solo se esaminati o confrontati con altri simili;

4) integrare la segnalazione con un breve commento che possa evidenziarne importanza e contenuti.

I dati dovranno essere fatti pervenire a:

Italia settentrionale:
Pierandrea Brichetti
via V. Veneto, 30
25029 Verolavecchia (BS)

Italia centro-meridionale (esclusa Calabria):
Emiliano Arcamone
Museo Provinciale di Storia Naturale
via Roma, 234
57127 Livorno

Sicilia e Calabria:
Bruno Massa
Istituto di Entomologia Agraria
viale delle Scienze, 13
90128 Palermo

Sardegna:
Helmar Schenk
via Valeggio, 1
09134 Cagliari Pini

Nella speranza che vorrete contribuire tutti alla buona riuscita dell'iniziativa, che ne fiancherà altre rivolte al rilancio del C.I.S.O., vi sollecitiamo a inviare, numerosi, i vostri dati di campagna più interessanti. Saranno attentamente esaminati dai vari responsabili ed elaborati per la pubblicazione da Emiliano Arcamone (coordinatore nazionale e responsabile).

La Direzione del C.I.S.O. e gli Editors di Avocetta vi ringraziano anticipatamente per la collaborazione.

Banca Dati Ornitologica per il territorio italiano

È stata realizzata una Banca Dati Ornitologica contenente circa 9000 informazioni bibliografiche che coprono il periodo 1959-1993.

Essa verrà commercializzata nel corso del 1994 al prezzo di Lire 3.000.000.

Le caratteristiche principali sono le seguenti:

- é costruita sulla selezione dei lavori scientifici riguardanti il territorio italiano pubblicati in Italia o all'estero dal 1959 al 1993.
- sono considerate le specie selvatiche appartenenti all'avifauna italiana, comprese quelle estinte, naturalizzate, ripopolate, re-introdotte o escluse.
- la pubblicistica scientifica selezionata comprende le riviste ornitologiche nazionale ed estere, i periodici di Musei di Storia Naturale, Istituti Universitari, Associazioni, Enti pubblici e privati, gli atti di Convegni, Seminari ecc. e gli atlanti degli uccelli nidificanti e svernanti
- è strutturata in modo che ogni record contenga le voci classiche di una citazione bibliografica (escluso il titolo), l'identificazione del taxon (nome scientifico e Codice Euring) e una scala gerarchica di parole chiave "argomenti" e "aree geografiche"
- le principali parole chiave "argomenti", distinte per specie nidificanti, svernanti e migranti, sono: Distribuzione, Popolazione, Ecologia, Biologia riproduttiva, Etologia, Sistematica, Genetica, Anatomia, Biometria, Alimentazione, Vocalizzazioni, Conservazione e Gestione, Tecniche di ricerca
- le parole chiavi "geografiche" sono elencate gerarchicamente dall'eventuale livello superiore (Regioni Zoogeografiche, Europa, Mediterraneo) a quello inferiore (Italia, Regioni). Sono incluse anche sottochiavi "geografico-ambientali" come Alpi,

Appennini, Padania, isole minori, centri urbani ecc.
- la BDO rappresenta uno strumento di lavoro versatile ed espandibile in quanto può essere facilmente personalizzata con l'aggiunta di ulteriore "chiavi" o di nuovi "campi"
- contiene circa 9000 records selezionati strutturati nei seguenti campi:

1 = Anno e categoria del periodico
2 = Codice Euring
3 = Nome scientifico del taxon
4 = Parole chiave "argomenti"
5 = Parole chiave "zone geografiche"
6 = Autore/i, anno di pubblicazione
7 = Periodico, volume, pagine
- l'acquisto della BDO garantisce nel futuro la possibilità di disporre di periodici aggiornamenti e di estensioni riguardanti la bibliografia "storica" (1900-1949)
- rappresenta uno strumento di lavoro indispensabile per ornitologi, Istituti universitari Musei di Storia Naturale ed Enti pubblici e privati direttamente o indirettamente impegnati nella ricerca, conservazione e gestione dell'avifauna
- viene fornita con un pratico Manuale che fornisce dettagliate spiegazioni sulla struttura e sulle possibilità dell'archivio e ne rende semplice e immediato l'utilizzo: può essere importata e gestita dai più diffusi Database utilizzabili con sistemi MS-DOS ® e Macintosh ®.

Pierandrea Brichetti
via V. Veneto, 30 - 25029 Verolavecchia (BS)

Request of informations: Pittas

Johannes Erritzoe is working on a new book, "The pittas of the world". The book is intended to summarise for each species all published and unpublished information of this very little known family (last monograph was Elliot's in 1985). A colour plate is planned for each of the 31 species and some other colour illustrations for the subspecies as well.

The author would welcome any unpublished or published information eg. trip reports, field observations with notes on habitat, identification tips, vocalizations, breeding records, descriptions of nest sites and nests, descriptions of the plumage of juveniles, behaviour or diet. Records of window-killed birds or dead by other accidents are of interest, also current status and populations everywhere, and possible treats for the survival of a species will be particularly useful. Even notes from captive birds will be of interest. Loaned photos used for reference will be returned in due course and contributions will be gratefully ackowledged in the book with full name and address. Please send any information on:

Johannes Erritzoe
House of Bird Research
Taps Old Rectory
DK-6070 Christiansfeld, Denmark

Proposal to found a European Ornithologists' Union

A number of ornithologists in Europe and around the world were contacted to discuss merits of starting a Continent-wide society for ornithology in Europe. After a generally positive response, a working commitee was formed to put this proposal into a more concrete form which could be circulated to potential members. This group met in July 1993 and came to the following conclusions.

Goals

A Union of ornithologists in Europe should serve to initiate, and encourage, collaboration between ornithologists on a Continent-wide basis, covering all aspects of ornithology from basic research to conservation. To do this, it should provide a forum for exchanging ideas and finding financial resources to support such aims. Its goals should in no way compete with, or replace, national institutions or specific organizations. On the contrary, it should simply enhance capacity to stimulate international collaboration between members. To achieve this forum for exchange, the committee suggests organizing biennial meetings in various European countries and initiating a scientific journal. This periodical should contain a wide range of contributions from review articles to original papers and news and notes about European ornithology; it is anticipated that the journal will, eventually, appear quarterly.

Proposed structure and time plan for development

The European Ornithologists' Union should be independent of national organizations and obligatory national representation. It should however, aim to maintain a wide geographical basis among members. The Union should be run by a democratically elected executive board and council, with members being appointed for four years. The aim of the working committee and many ornithologists contacted is to set up a preparatory committee at the XXI International Ornithological Congress in Vienna, August 20-25, 1994. Thereafter, it is intended to have an inaugural meeting in 1995 and at the same time begin publication of the journal. The members of the working committee, mentioned below, would appreciate any ideas or comments on this proposal. At the same time they would like to set up a mailing list of prospective members. Therefore, please address any comments, or send your wish to be placed on the mailing list to one of the members of the Working Committee of the E.O.U.P.: F. Bairlein, P. Berthold, C. Bibby, J. Blondel, J. Dittami, L. Jenni, B. Leisler, E. Matthysen, C. Perrins, F. Spina and H. Winkler.

Fernando Spina
Istituto Nazionale per la Fauna Selvatica
Via Cà Fornacetta, 9 - 40064 Ozzano Emilia (Bo)

Norme per gli autori

AVOCETTA pubblica articoli originali, brevi note, sintesi di aggiornamento, commenti, corrispondenze e recensioni, su argomenti che coprono l'intero campo dell'ornitologia. Verrà tuttavia data la preferenza a lavori sperimentali sull'ecologia, l'etologia, la zoogeografia della fauna ornitica della regiona mediterranea e delle zone alpine.

I lavori sottoposti saranno valutati da referees e, in conseguenza dei suggerimenti da loro effettuati, saranno accettati, rinviati agli autori con proposte di modifiche, o respinti. Tale decisione è competenza definitiva degli *editors*.

I lavori sottoposti in italiano, inglese o francese, devono essere dattiloscritti con interlinea 2, ampi margini, su una sola facciata e devono essere forniti in **tre** copie, complete di illustrazioni. L'autore indicherà a matita sul margine sinistro del dattiloscritto la posizione in cui illustrazioni e tabelle vanno inserite nel testo.

Il testo degli articoli dovrà essere diviso come segue:
- Titolo
- Cognome e nome dell'Autore
- Indirizzo dell'Autore
- Testo del manoscritto, diviso nei seguenti capitoli: Riassunto, Introduzione, Metodi, Risultati, Discussione, Ringraziamenti, Riassunto in lingua diversa da quella dell'articolo, Bibliografia
- Tavole e figure

Il **riassunto** iniziale, di un massimo di 40 righe, elencherà schematicamente tutti i problemi trattati ed i risultati ottenuti senza riferimento diretto al testo e senza ripetere l'informazione contenuta nel titolo. Nel riassunto non devono comparire abbreviazioni e simboli specialistici.

Il problema principale affrontato nel lavoro va esposto chiaramente nell'**introduzione** senza eccessivi dettagli storici. La continuità con altre ricerche va posta in evidenza con gli opportuni riferimenti bibliografici evitando la ricapitolazione di questi stessi lavori. I metodi devono essere espressi con chiarezza ma senza introdurre dettagli particolareggiati, tranne quando si tratti di un lavoro metodologico innovativo.

I nomi **di genere e di specie** e le parole da evidenziare devono essere sottolineati (per il carattere corsivo). I nomi comuni di animali vanno scritti maiuscoli.

Le **citazioni bibliografiche** nel testo possono essere date come: Mayr (1963), Andrewartha e Birch (1984), Fasola *et al.* (1987) o alla fine della frase (Mayr 1963, Fasola *et al.* 1987).

Le citazioni devono conformarsi ai seguenti esempi:

Capitolo: Baldaccini N.E., Benvenuti S., Fiaschi V., Ioalé P. e Papi F. 1982. Pigeon orientation: experiments on the role of olfactory stimuli perceived during the outward journey. In: Papi F. e Wallraff H. G., Edits. Avian navigation. Springer, Berlin pp. 160-169.

Libro : Lack D. 1954, The natural regulation of animal numbers. Clarendon Press, Oxford.

Rivista : Papi F. 1986. Pigeon navigation: solved problems and open questions. Monit. Zool. ital. (N.S.) 20: 471-571.

I titoli delle riviste devono essere abbreviati secondo l'ultima edizione (quarta) del World List of Scientific Periodicals (1960) e i supplementi della British Union-Catalogue of Periodicals o le Serial Publications in the British Museum (Natural History) Library. Nel dubbio scrivere il riferimento in estenso. Non includere materiale non pubblicato tra le citazioni.

Le **Tavole** devono essere numerate consecutivamente con i numeri arabi e battute su un foglio separato con una chiara ed esauriente legenda.

Illustrazioni. Il massimo del formato (legenda inclusa) è 178 x 214 mm. Le illustrazioni devono essere 1.5-2 volte più grosse del formato definitivo. Anche le figure vanno numerate con numeri arabi. Scritte, lettere e numeri delle figure devono essere sufficientemente grosse da essere lette dopo riduzione del formato. Disegni e grafici in china nera devono essere fatti su carta bianca o da lucido. Assieme all'originale vanno spedite tre copie.

Sono richieste quattro copie di fotografie.

Legende di fotografie e figure vanno scritte su foglio separato.

Cinquanta estratti di ciascun articolo sono inviati gratis. Ulteriori copie possono essere acquistate con buono d'ordine allegato alle bozze di stampa.

I manoscritti vanno spediti a:
Redazione di AVOCETTA,
Dipartimento di Biologia Animale,
via Accademia Albertina 17 - 10123 TORINO.

Instructions to authors

AVOCETTA publishes original articles, short communications, reviews surveys, comments and correspondence on all topics of ornithology. However, preference will be given to original works in the ecology, ethology and zoogeography of the ornithological fauna in the Mediterranean region and the Alpine area.

Manuscripts, conforming to the journal's scope, are subject to the review process, and the final decision concerning acceptance or rejection will be made by the Editors.

Manuscripts shoud be submitted in triplicate preferably in English (Italian and French are also accepted). They must be typewritten double spaced with wide margins. Position of figures and tables should be marked on the margin.

Manuscripts should be arranged as follows:

- — Title
- — Author's names and initials
- — Address of author's institution
- — Text of the paper, divided into the following sections: Abstract, Introduction, Methods, Results, Discussion, Acknowledgements, Abstract (in a language different from that of the text), References
- — Tables and illustrations

The **abstract**, of max 40 lines, should give concise but exhaustive information on the problem and the results, and be intelligible without reference to the main text. Abstract need not repeat information given in the title.

Abbreviations and special symbols must not appear in the abstract.

The main problem should be outlined briefly in the **introduction**, and detailed historical introductions should be avoided. Continuity with earlier work on the subject should be established by reference to recent papers, which need not themselves be summarized. Experimental methods must be clearly set out, but detailed descriptions of methods are of value only if they convey substantially new information.

Genus and species names and words to be emphasized should be underlined once (for italics). The common names of animals should be capitalized.

Literature citations in the text should be given as: Mayr (1963), Andrewartha and Birch (1984), Fasola *et al.* (1987) or, at the end of a sentence, (Mayr 1963, Fasola *et al.* 1987).

References at the end of the paper should be listed in alphabetical order by the first author's name; all work referred to in the text should be listed, and only those.

References should be conformed to the following examples.

Chapter:	Baldaccini N.E., Benvenuti S., Fiaschi V., Ioalé P. and Papi F. 1982. Pigeon orientation: experiments on the role of olfactory stimuli perceived during the outward journey. In: Papi F. and Wallraff H. G., Edits. Avian navigation. Springer, Berlin pp. 160-169.
Book :	Lack D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.
Journal :	Papi F. 1986. Pigeon navigation: solved problems and open questions. Monitore Zool. Ital. (N.S.) 20: 471-517.

Titles of journals should be abbreviated according to the last (4th) edition of the World List of Scientific Periodicals (1960) and following supplementary lists issued by the British Union-Catalogue of Periodicals or the Serial Publications in the British Museum (Natural History) Library. If in doubt, give the title in full. Do not include unpublished material among the references.

Tables must be numbered consecutevely in arabic numerals and typed on a separate sheet together with a clear descriptive legend.

Illustrations. The maximum dimensions of published figures (including the legend) are 178 × 241 mm. Authors are requested to submit illustrations 1.5-2 times larger than the final format. Illustrations should be numbered in Arabic numerals.

Lettering should be big enough to remain clearly visible after reduction. Drawings should be in black ink on drafting paper. The original and three copies should be submitted.

Photographs should be submitted in quadruplicate. The legend of both figures and photographs should be typed separately from the rest of the manuscript.

Fifty (50) offprints of each paper are supplied free of charge. Additional offprints can be purchased, provided the order is received with the corrected proofs.

Manuscripts should be addressed to:

The Editors, AVOCETTA,
Dipartimento di Biologia Animale,
via Accademia Albertina 17 - 10123 TORINO, Italy.

AVOCETTA

N° 2, Vol. 17 - December 1993

CONTENTS

Indexed in Animal Behavior Abstracts, Ecology Abstracts, Zoological Records.