

THE GREBES OF MADAGASCAR ¹⁾

by

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INTRODUCTION

The grebes of Madagascar present a problem of both systematic and ecological interest. Three species of grebes are known to occur in Madagascar (DELACOUR 1933, where they are illustrated in colour; RAND 1936; see also, Plate I). All of these belong to the group of small grebes known as dabchicks, and are of approximately the same size. Two species are known to breed on the island, both of these being regarded as species endemic to Madagascar (*Podiceps pelzelinii*, *P. rufolavatus*). A third species has been recorded only rarely in Madagascar (*P. ruficollis*; the few specimens known belong to the continental African race *capensis*). This situation is the more interesting since *Podiceps ruficollis* is widely spread over the whole of the Old World land masses, where, apart from Australia, it is the only species of dabchick to occur. Its recorded absence as a breeding bird in Madagascar is quite unexpected. *Podiceps pelzelinii*, known since its description by HARTLAUB in 1861, is reported to occur in all fresh water habitats throughout Madagascar; it has a colour pattern which sets it apart from any other of the small grebes. *Podiceps rufolavatus* was first collected in 1929 and subsequently described by DELACOUR in 1932. It is known from one locality in Madagascar (*Lake Alaotra*). According to DELACOUR (1933) *Podiceps rufolavatus* occurs in two colour phases, a fact, which, in view of the restricted species' range is most remarkable.

The problem of the Madagascar grebes therefore is not only that of GAUSE's principle relating to the ecology of similar species of approximately equal size living in more or less similar habitats, but also that of the geographical origin of avian members of the Madagascar avifauna in general and the subsequent processes of species formation.

In 1960, Mrs. H. A. W. PAYNE (then, Miss H. A. W. SMIT) assistant at the Zoological Museum of the University of Amsterdam, stayed over twelve weeks in Madagascar to collect specimens and data on the distribution and ecology of these species of grebes.

¹⁾ Read in summary at the Second Pan-African Ornithological Congress, Pietermaritzburg, South Africa, 23 September 1964.

ITINERARY AND ACKNOWLEDGEMENTS

Mrs. H. A. W. PAYNE stayed in Madagascar from 1 May 1960 - 27 July 1960, where she undertook field-studies in and around the following localities.

May 1-4. Tamatave—no grebes seen.

May 4-23. Tananarive—marshes and small lakes: Imerimanjaka marsh, Lake Mandroseza, Androndrakely marsh, Lake Lohazozoro.

May 23-June 14. Lake Alaotra in northeast Madagascar, at about 750 m above sea level. As this is the type locality of *Podiceps rufolavatus*, the main work was concentrated in this area. The lake is about 35 km long and averages 5 km wide; it is rather shallow, with broad fringing reed zones mainly composed of *Cyperus madagascariensis*.

June 14-25. Andilamena, about 30 km north of Lake Alaotra, and ca. 900 m above sea level: many small marshes, lakes and barrages, among which is Lake Antsimangana (water sheet of about 10 km² extent).

June 25-July 11. Lake Alaotra.

July 11-22. Tananarive and Lake Itasy (a volcanic lake, 80 km west of Tananarive, of about 50 square km extent, and ca. 1250 m above sea level), and Lake Mantasoa (an artificial lake, 25 km east of Tananarive, of about 30 square km extent, and ca. 1500 m above sea level).

July 22-27. Tamatave.

Mrs. PAYNE managed to collect 44 specimens of the three grebes mentioned above, all of these having been deposited in the Zoological Museum of the University of Amsterdam. She wishes to acknowledge most kind and effective help from Madagascar officials, including directors and staff of the *Institut des Recherches Scientifiques de Madagascar* (IRSM) at Tananarive and the *Institut des Recherches Agronomiques de Madagascar* (IRAM) on Lake Alaotra, where in addition she received kind hospitality. She is also grateful to the *Studiefonds voor Zuid-Afrikaanse Studenten*, the *Netherlands Organisation for the Advancement of Pure Research* (ZWO), the *Fonds Doctor Catharine van Tussenbroek*, and last but not least to Professor Dr. H. ENGEL, Director of the Zoological Museum of Amsterdam, all of whom made her African journey possible.

This study was intended as part of a doctoral thesis on the geography and species formation in grebes under the direction of the senior author.

The authors wish to extend their thanks to the late Dr. G. C. A. JUNGE of the Leiden Museum, to Dr. J. BERLIOZ and Dr. J. DORST of the Paris Museum, to Mr. J. D. MACDONALD and Mr. C. J. O. HARRISON of the British Museum (Natural History), to Dr. D. AMADON of the American Museum of Natural History, New York, and to the officials of the museums at Cape Town and Bulawayo, for hospitality and loan of specimens.

Dr. J. BERLIOZ, Dr. H. N. KLUIJVER, Dr. G. F. MEES, and Dr. R. W. STORER were so kind to read the first draft of the manuscript; the authors thankfully acknowledge their kind and constructive comments. Still, the sole responsibility for the contents of this paper remains with the authors.

Mr. C. B. PAYNE kindly corrected the grammar of a large part of the manuscript.

SCOPE OF THE PAPER

The paper presents the description of the specimens of Madagascar grebes collected by Mrs. PAYNE and a comparison of these with previously collected material present in the *Muséum national d'histoire naturelle* in Paris and the *British Museum (Natural History)* in London, and the *American Museum of Natural History* in New York (mainly from the *Mission Franco-Anglo-Américaine*, 1929-1931), and in other museum collections. The authors are most thankful to the curators of these museums for help received.

A comparison of the structural characters of the species is made and data are given on the distribution and the ecology of the species as observed by Mrs. PAYNE. Finally a theory is developed on the geographic history and species formation of the grebes in Madagascar and a tentative prognosis is given of their future development.

Podiceps pelzelni Hartlaub

Numerous specimens of this species are known in various collections. DELACOUR (1933) and RAND (1936) report it as common throughout the island in suitable habitats. Birds in breeding plumage are easily distinguished by the black cap, greyish sides of the head and neck which merge gradually into a variable amount of rufous bordering the ear coverts and extending down the sides of the neck as an indistinct and usually short line. Between the black cap and the grey of the head there is a distinct line of white. This line, and the rufous colour of the head are absent in immature (or non-breeding?) birds. The under parts are white and there is a sharp line of demarcation between the white of the abdomen and the grey of the breast. The flanks and the lower abdomen are equally light grey. This species has no swollen and conspicuously coloured patch at the base of the bill during the breeding time (Plate I).

Mrs. PAYNE did not succeed in collecting more than 5 specimens, only one of which being in fully adult breeding plumage with a black bill with light tip (nr. 17060, Lake Alaotra, 5 July 1960). The remaining four specimens have a mainly yellowish bill, or are lacking the reddish brown patches on the sides of the head and neck. A summary of the measurements of 28 adult specimens examined in addition in the museum collections in Leiden, London, Paris and Tananarive follows below.

Wing ¹⁾	♂	101 - 106	average (10)	103.0 mm
	♀	93 - 105	average (14)	99.0 mm
Bill ²⁾	♂	18 - 24	average (10)	21.8 mm
	♀	18 - 21	average (13)	18.9 mm
Tarsus	♂	36 - 39	average (6)	37.5 mm
	♀	33 - 39	average (15)	35.8 mm
Middle toe ³⁾	♂	42 - 48	average (5)	45.1 mm
	♀	40 - 46	average (13)	42.7 mm
Bill/wing × 100				
	♂	21 %	- ♀	19 %
Bill/tarsus × 100				
	♂	54 %	- ♀	53 %
Middle toe/tarsus × 100				
	♂	120 %	- ♀	119 %
Tarsus and middle toe/bill × 100				
	♂	80 %	- ♀	79 %

Specimens with flesh-coloured bills, usually with dark patches on the upper mandible and at the base of the lower mandible, have been considered as not fully adult. With the exception of one male (nr. 17039, Lake Alaotra, 26 May 1960), all light-billed birds collected by Mrs. PAYNE lacked the reddish brown sides of the neck.

Iris, in freshly collected specimens, dark red (3 ♂, 1 ♀; PAYNE), once reddish-brown (1 ♂ with almost wholly fleshy-yellow bill; PAYNE).

Feet yellowish green.

Podiceps rufolavatus Delacour

Birds in breeding plumage have the crown of the head and hind part of the neck black, the feathers having a greenish gloss and those on the nape being slightly elongated. As a result the black cap contrasts sharply with the light colour of the sides of the head. The latter have a more or less uniform coloration of light buff or light greyish buff growing darker towards the sides of the head and neck. There is a distinct, but not sharply defined dark patch extending from the base of the lower mandible to somewhere below the eye. The chin is white or very pale buff. The under parts are rather dark, being some shade of reddish or greyish brown with a light centre on the abdomen; the breast, the flanks, and the lower abdomen are darkest grey. The outer webs of the lesser wing coverts show considerably less white than in *ruficollis* and are largely brownish. This character is, however, hard to express quantitatively and is therefore not used in the further discussion.

Hitherto this species seems to have been known mainly from 15 specimens collected between 30 May and 7 June 1929 by members of the

¹⁾ Measured when pressed flat on the ruler.

²⁾ Exposed culmen.

³⁾ Including claw.

combined French, British and American Expeditions to Madagascar, 14 specimens of which having been examined by the authors.

Mrs. PAYNE collected 10 specimens in breeding plumage, all of them with a black, light-tipped bill, and a light, swollen patch of yellowish-green at the base of the bill, permitting an easy specific identification (Plate II). These birds show, for small grebes, remarkably little individual variation in coloration and in this respect do not substantiate DELACOUR's (1933) assumption of the presence of two colour phases (see, however, below). Additional birds in different, non-breeding or immature plumages do not allow an easy identification and will be discussed separately. Mrs. PAYNE collected all her specimens at Lake Alaotra, between 28 May and 6 July 1960. The measurements of these birds follow below.

Wing ♂, 91, 91, 92, 94, 94; ♀, 89, 90, 91, 93 mm.

Bill ♂, 25, 25, 26, 26, 27; ♀, 22, 23, 25, 25 mm.

Tarsus ♂, 36, 36, 37, 37, 37, 39; ♀, 34, 34, 36, 38 mm.

Middle toe ♂, 44, 45, 45, 46, 47, 48; ♀, 43, 44, 45, 46 mm.

Body weight ♂, 180, 190, 200, 200, 210, 210; ♀, 160, 175, 205, 230 grams.

A summary of the measurements of 20 specimens in breeding plumage including those preserved in the museums in Paris, London, and New York, gives the following result:

Wing	♂	90 - 95	average (9)	92.6 mm
	♀	89 - 93	average (9)	91.4 mm
Bill	♂	25 - 27	average (9)	25.9 mm
	♀	21 - 25	average (9)	23.1 mm
Tarsus	♂	35 - 39	average (10)	36.9 mm
	♀	34 - 38	average (10)	34.9 mm
Middle toe	♂	42 - 48	average (10)	45.4 mm
	♀	42 - 46	average (10)	43.8 mm
Bill/wing × 100				
	♂	28 %	-	♀ 25 %
Bill/tarsus × 100				
	♂	70 %	-	♀ 66 %
Middle toe/tarsus × 100				
	♂	123 %	-	♀ 126 %
Tarsus and middle toe/wing × 100				
	♂	89 %	-	♀ 86 %

Iris, in freshly collected specimens, light yellow (6 ♂, 4 ♀, PAYNE).
Feet greyish green.

Podiceps ruficollis (Pallas)

DELACOUR (1933) could trace the presence of no more than 5 specimens collected in Madagascar, probably all of these dating from the 19th century. The collection of his Mission to Madagascar (1929-1931) did not contain specimens of this species at all (DELACOUR 1932)! MILON (1946) is the first and so far the only author to record this species in Madagascar in numbers. Between the end of October until December

1945 (and apparently onwards) he estimated ca. 150 birds to be present on Lake Anosy near Tananarive. His observations have been substantiated by pictures (*op. cit.*: Pl. I) and by a collected specimen, now in the Paris Museum.

Mrs. PAYNE collected 10 specimens in various stages of breeding plumage, which leave no doubt of a correct specific identification. Specific characters are a large black chin-spot which is connected with a dark spot below the eye, and reddish-brown sides of the head and neck which leaves only a narrow black line on the hind neck. Birds collected in non-breeding or immature plumages have not been included here and will be discussed separately. The bill is black with a small light tip; two specimens have some small lighter patches of yellowish-brown on the lower mandible. There is a swollen and large patch of yellowish-green at the base of the lower mandible, which is smallest in the specimens with a not wholly black bill (Plate I).

The ten specimens mentioned above originated from Lake Alaotra (4), Lake Itasy (2), and several other localities. The dates of collecting lay between 15 May and 20 July 1960. In coloration the birds do not differ from a series of 11 *P. ruficollis capensis* in breeding plumage collected by Mrs. PAYNE in South Africa; three specimens have the underparts extensively washed with blackish grey, one of these being almost wholly dark underneath (♂, Lake Itasy, 14 July 1960). None of the South African birds is as dark.

Madagascar birds differ slightly from continental African ones in the measurements of the wing and bill. A summary of the measurements is given below.

Madagascar:

Wing ♂, 95, 97, 99, 105; ♀, 92, 95, 96, 99 mm.
Bill ♂, 21, 21, 21, 21, 22, 23; ♀, 19, 20, 20, 20 mm.
Tarsus ♂, 35, 36, 36, 37, 37, 38; ♀, 34, 34, 35, 35 mm.
Middle toe ♂, 42, 44, 46, 46, 46, 47; ♀, 41, 43, 43, 47 mm.
Body weight ♂, 185, 195, 200, 205, 225, 230; ♀, 165, 170, 170, 185 grams.

South Africa:

Wing ♂, 100, 103, 105, 107; ♀, 95, 96, 100, 101, 101, 102 mm.
Bill ♂, 19, 20, 21, 21; ♀, 18, 18, 18, 19, 19, 19 mm.
Tarsus ♂, 36, 36, 36, 38; ♀, 33, 34, 36, 36, 36, 38 mm.
Middle toe ♂, 42, 43, 43, 44; ♀, 42, 42, 43, 43, 44, 45 mm.
Body weight ♂, 195, 195, 210, 210; ♀, 145, 145, 170, 190, 200, 210 grams.

Recently collected material of *P. ruficollis* from other sources include two specimens in breeding plumage from Lake Alaotra (September 1931 and 15 June 1950) in the *Institut des Recherches Scientifiques de Madagascar* (IRSM) at Tananarive examined by Mrs. PAYNE, and one specimen

in breeding plumage from Tananarive (27 July 1946, collected by MILON) in the Paris Museum, examined by VOOS (see above, and cf. MILON 1946 : 85).

When all data are combined the measurements and proportions of *P. ruficollis* from Madagascar are as follows (the average measurements of 19 continental African males and 29 females are added in parentheses).

Wing	♂	95 - 105	average (5)	98.2 mm (102.4)
	♀	92 - 101	average (5)	96.6 mm (98.3)
Bill	♂	21 - 23	average (7)	21.6 mm (20.2)
	♀	19 - 20	average (5)	19.7 mm (18.4)
Tarsus	♂	34 - 38	average (7)	36.1 mm (36.1)
	♀	34 - 35	average (5)	34.7 mm (35.1)
Middle toe	♂	42 - 47	average (6)	45.2 mm (43.5)
	♀	41 - 47	average (5)	43.7 mm (42.1)
Bill/wing × 100				
	♂	22 %	(20 %)	- ♀ 20 % (19 %)
Bill/tarsus × 100				
	♂	60 %	(56 %)	- ♀ 57 % (52 %)
Middle toe/tarsus × 100				
	♂	125 %	(121 %)	- ♀ 126 % (120 %)
Tarsus and middle toe/wing × 100				
	♂	83 %	(78 %)	- ♀ 81 % (79 %)

Iris, in freshly collected specimens, brown (4 ♂, 4 ♀), once dark red-brown (♂), and once brown with light brown outer circle (♂) (PAYNE).

In birds from the African continent the iris was found to be brown or dark brown (3 ♂, 3 ♀, PAYNE). Other collectors also have usually indicated the colour of the iris as some shade of brown, or reddish brown; once a label mentioned "dull yellow" (Lake Maraye, Uganda), and once "yellowish" (North Rhodesia).

Feet greyish green, once dark grey (PAYNE).

INTERMEDIATES BETWEEN *P. rufolavatus* AND *P. ruficollis*

Mrs. PAYNE's series include 5 birds in adult plumage, which in the plumage characters are more or less intermediate between *P. rufolavatus* and *P. ruficollis*. A short description follows below. The sequence of the specimens is from that mostly resembling *rufolavatus* to that mostly resembling *ruficollis* (Plates III and IV). The characters which do *not* correspond with those of the species mentioned for direct reference in each case have been printed in *italics*.

Nr. 17064. ♂. Lake Alaotra, 6 July 1960. Like *rufolavatus*, but with a *large grey chin-spot*, formed by broad dark basis of the feathers, which in some cases are edged with white. Bill black with white tip; rather large swollen spot at base of bill. *Iris brown*. Feet greenish grey. Wing 95, bill 26, tarsus 36, middle toe 45 mm.

Nr. 17037. ♂. Lake Alaotra, 26 May 1960. Like *rufolavatus*, but with more of a *pale rufous* on the sides of the neck and also somewhat *more rufous* on the sides of the head; *chin slightly spotted with dark grey* on the basis of the feathers.

Colour of bill and feet not indicated. Large swollen spot at base of bill. Iris light yellow. Wing 98, bill 24, tarsus 36, middle toe 45 mm.

Nr. 17067. ♀. Lake Alaotra, 7 July 1960. Like a *short-billed* and *pale-brown-faced rufolavatus* with *dark spotted chin* and dark grey spot below the eye. Bill dark grey; basal and lower part of lower mandible flesh colour; small swollen spot at base of bill. Iris light yellow with some grey. Feet greenish grey. Wing 98, bill ca. 22, tarsus 36, middle toe 46 mm.

Nr. 17032. ♂. Lake Alaotra, 24 May 1960. Like a *brown-faced* (pale rufous) *rufolavatus* with *dark grey chin patch* connected with a large black spot below the eye. Bill black with light tip; large swollen spot at base of bill. Iris dark yellow. Colour of feet not indicated. Wing 95, bill 24, tarsus 38, middle toe 45 mm.

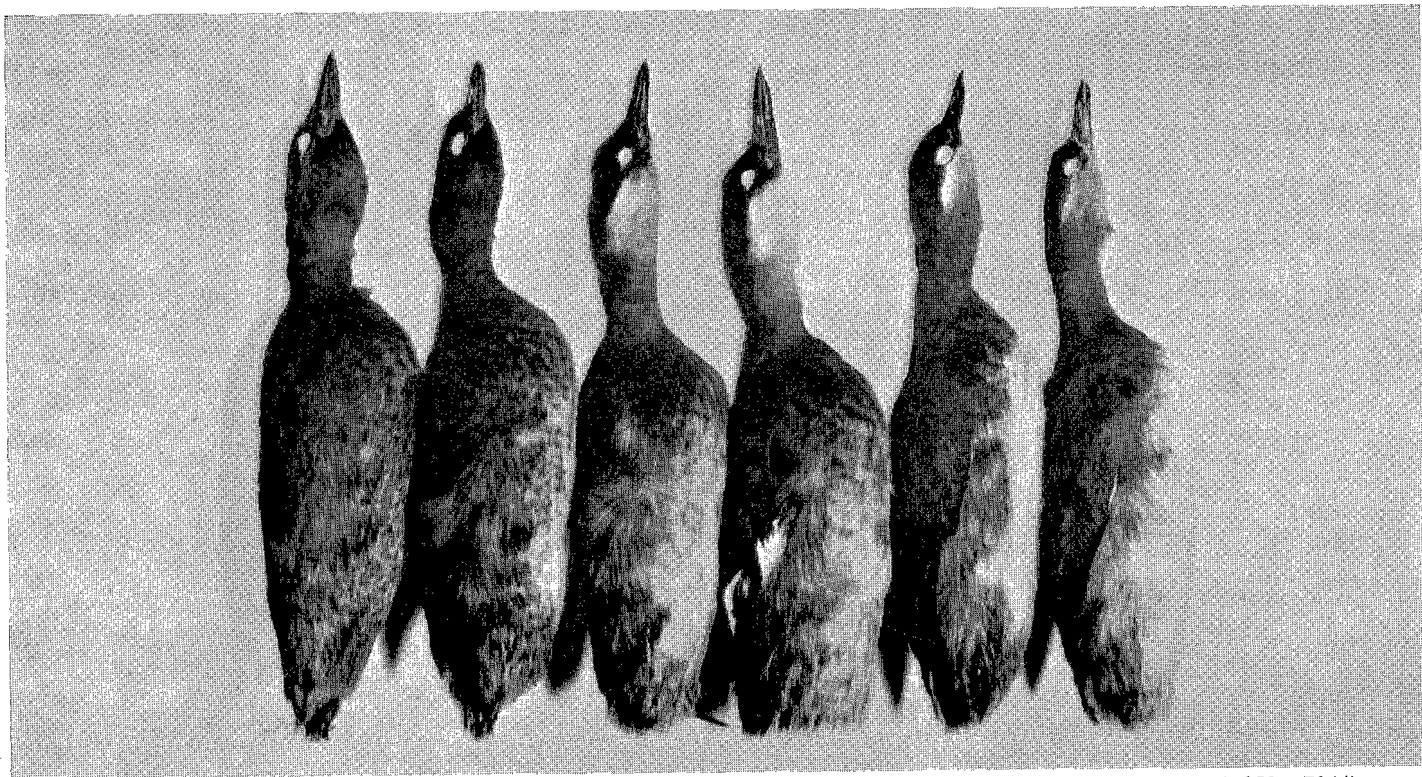
Nr. 17066. ♀. Lake Alaotra, 7 July 1960. Like a *long-billed ruficollis* with slightly paler, more buffish brown, less rufous sides of the head, and large though ill-defined dark spot on chin and below the eye. Bill black with light tip; large swollen spot at base of bill. *Iris light yellow with some grey*. Feet dark grey. Wing 102, bill 23, tarsus 37, middle toe 46 mm.

BIRDS IN NON-BREEDING AND IMMATURE PLUMAGES (Tables 1 and 2)

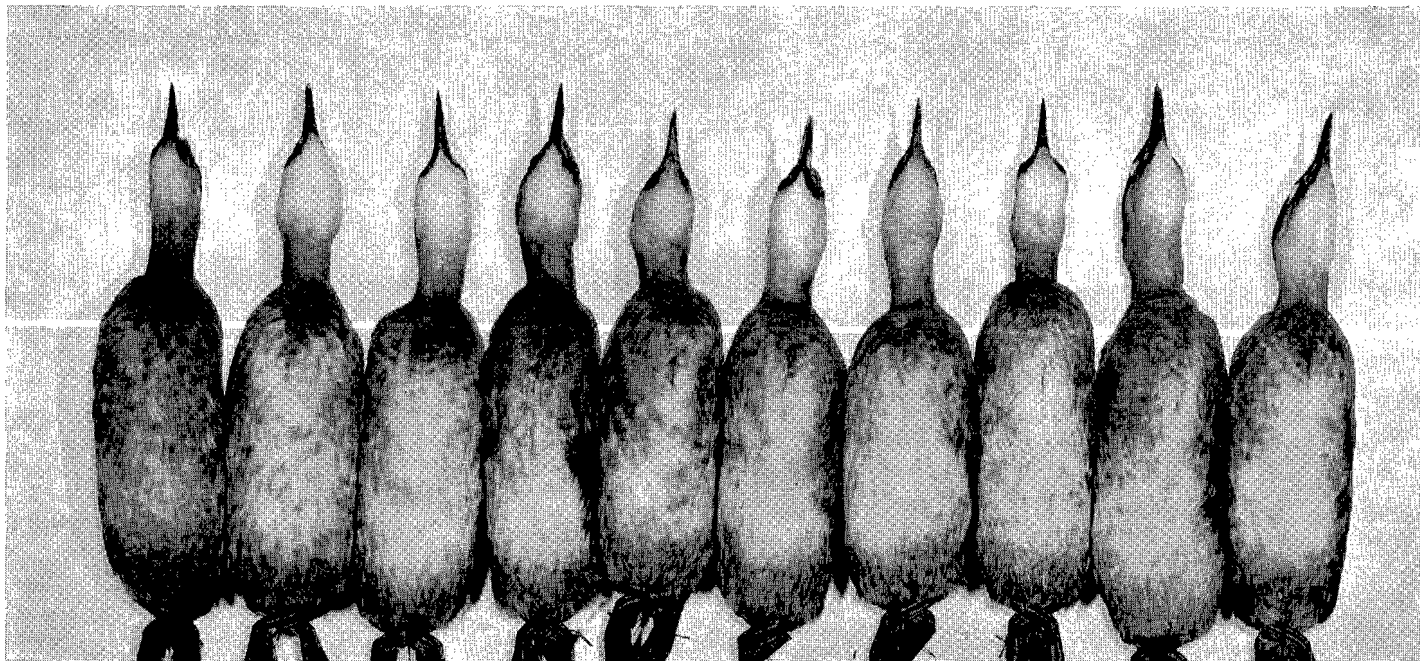
Mrs. PAYNE collected 14 specimens of *P. rufolavatus* and *P. ruficollis* in non-breeding or immature plumages. Some of these with heavily marked and spotted heads show various stages of immaturity. Others which lack some of the bright coloration of the nuptial plumage have been considered as non-breeding, but this series of specimens in incomplete plumage may also include immature birds. In view of the presence of adult intermediates, it is not easy, and it may perhaps be impossible, to assign all of the immature specimens to either *rufolavatus* or *ruficollis*. Mrs. PAYNE did not succeed in collecting juvenile, striped-headed specimens of *P. pelzelinii*.

Among the series mentioned above there are three which show all characters of adult *rufolavatus*, in addition to some irregular dark spots on the sides of the head, and juvenile, downy feathers on the abdomen (nrs. 17041 and 17036; Plate V), or only being somewhat duller in coloration and with downy feathers left on the lower abdomen (nr. 17063; Plate V). All three are fully grown birds. They are considered as *P. rufolavatus*.

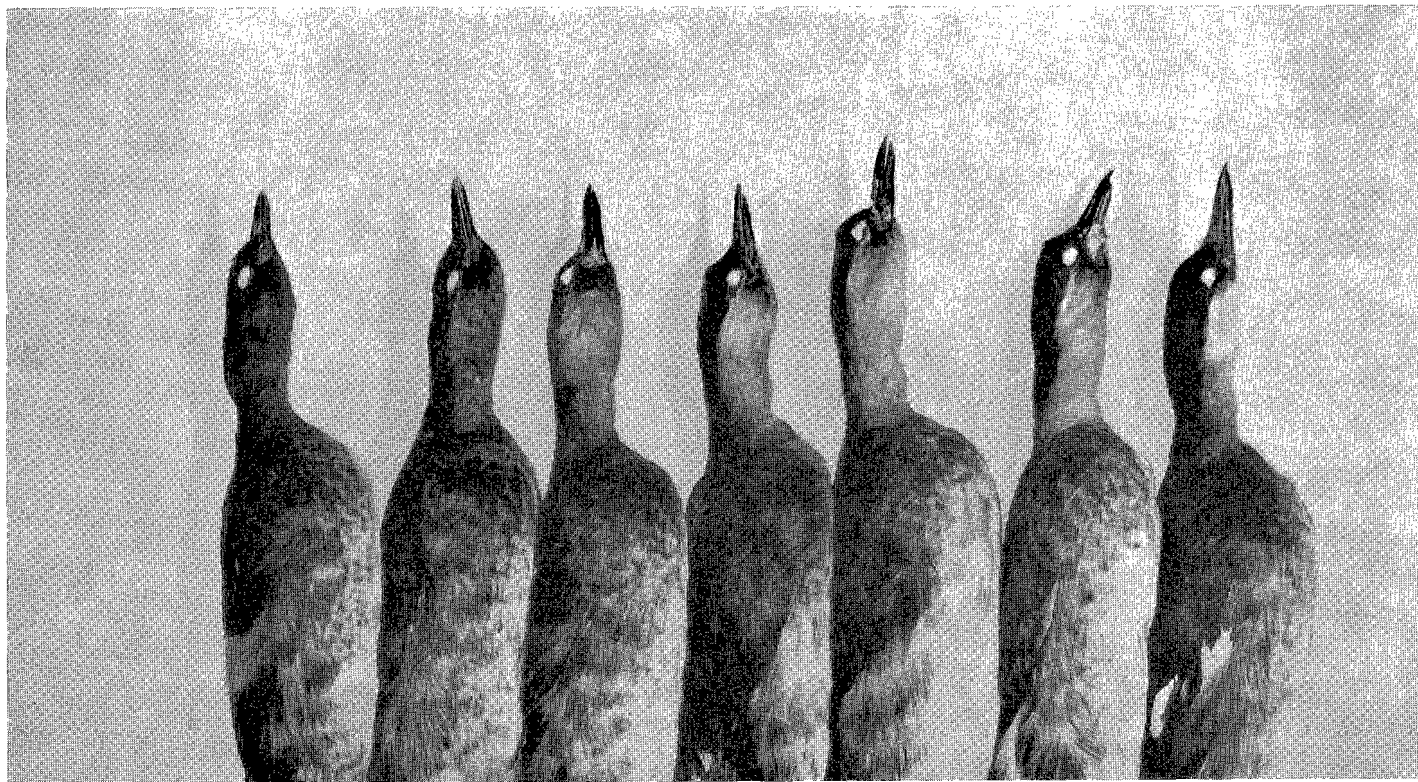
Two specimens are in almost full grown juvenile plumage with heavily striped and spotted head and neck. One is indistinguishable from juvenile specimens of *P. ruficollis* from continental Africa; it has the thicker and shorter bill of that species and has rufous brown spots above the eye, on the nape and on the neck (nr. 17031; Plate VI). The specimen, which apparently is too young to have made extensive flights, if any, is considered as proof of the breeding of *P. ruficollis* in Madagascar.



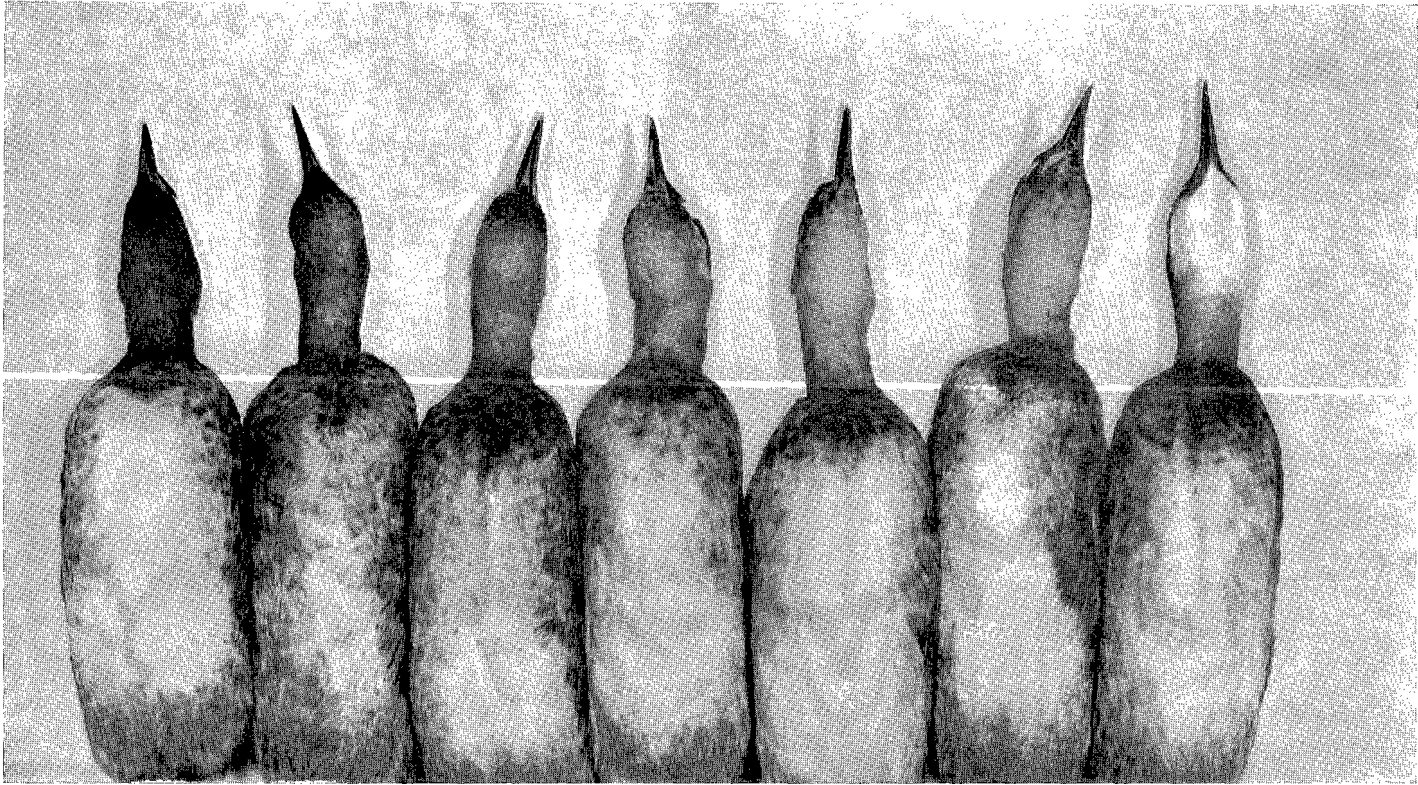
Three species of Madagascar grebes. From left to right: *Podiceps ruficollis* (nrs. 17069, 17030), *P. rufolavatus* (nrs. 17050, 17044), *P. pelzelni* (nrs. 17039, 17060).



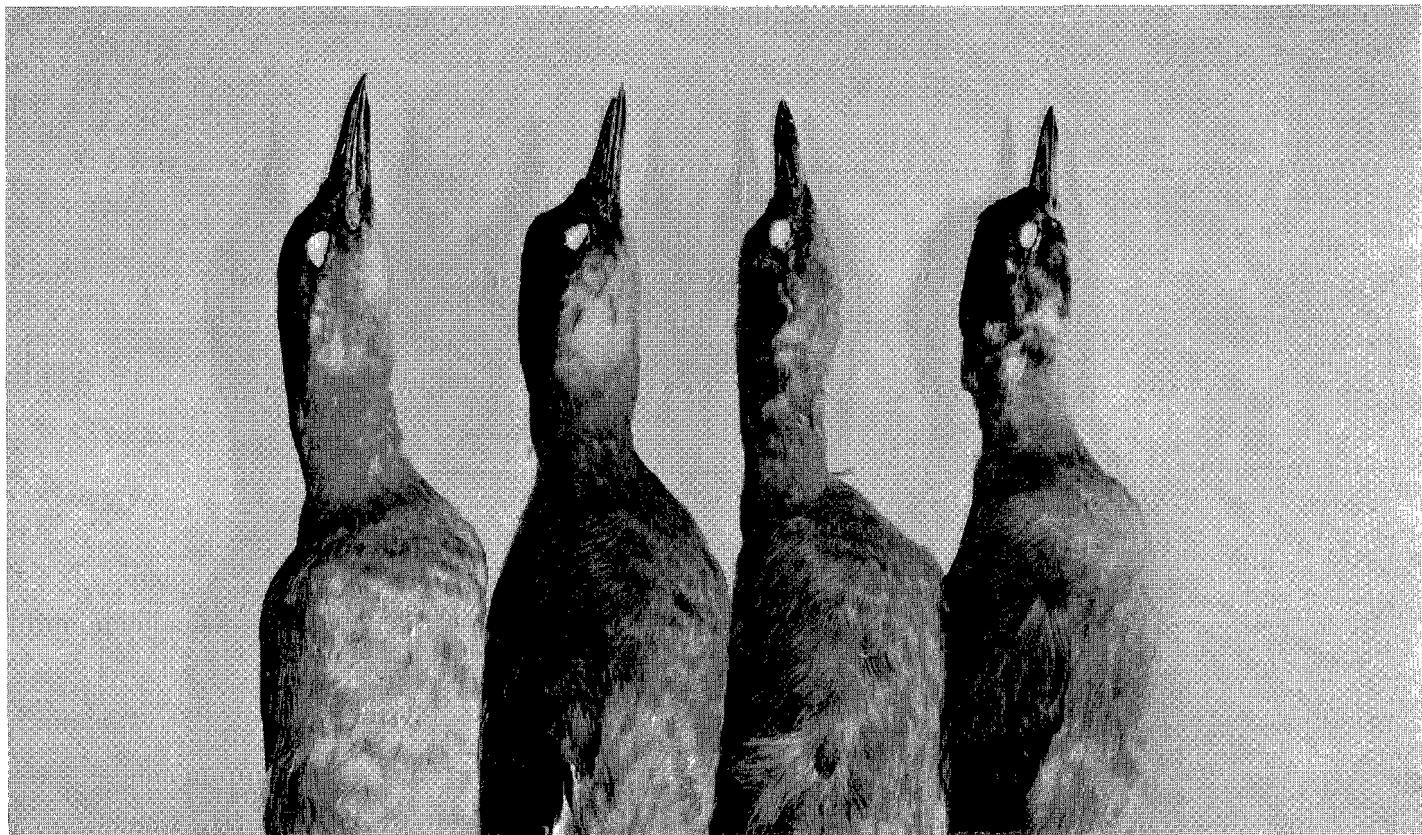
Series of *Podiceps rufolavatus* in adult breeding plumage collected by Mrs. PAYNE on Lake Alaotra, Madagascar, 28 May-6 July 1960.
From left to right: nrs. 17040, 17042, 17044, 17046, 17048, 17049, 17050, 17057, 17061, 17062.



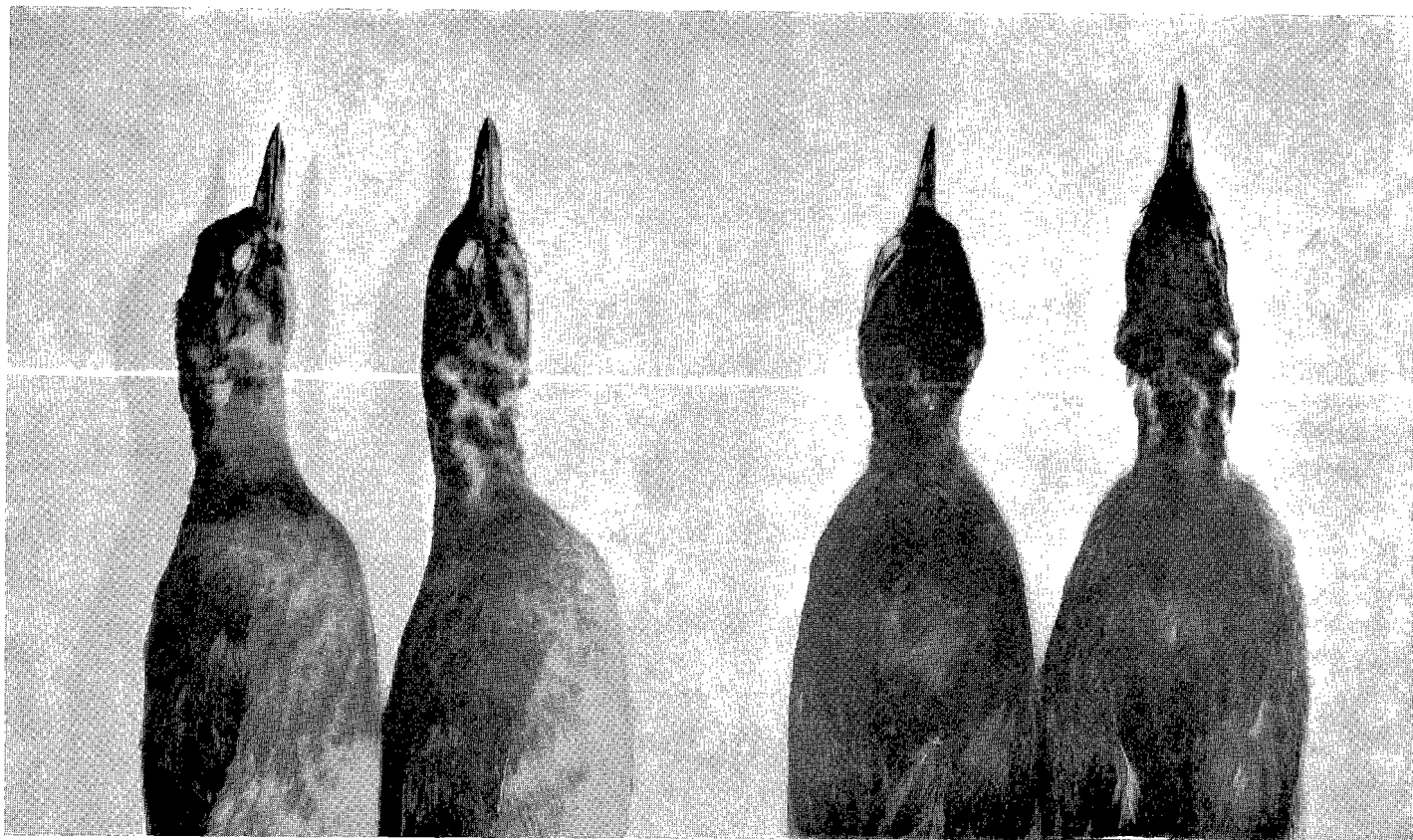
Supposed hybrids of *Podiceps rufolavatus* and *Podiceps ruficollis* in Madagascar. From left to right: *P. ruficollis* (17030), hybrids (nrs. 17066, 17032, 17067, 17037, 17064), *P. rufolavatus* (nr. 17044).



Supposed hybrids of *Podiceps rufolavatus* and *Podiceps ruficollis* in Madagascar. From left to right: *P. ruficollis* (17030), hybrids (nrs. 17066, 17032, 17067, 17037, 17064), *P. rufolavatus* (nr. 17044).



Immature grebes from Madagascar, tentatively referred to *Podiceps rufolavatus*. From left to right: nrs. 17063, 17041, 17036, 17077.



Juvenile grebes from Madagascar: left, lateral view; right, dorsal view. The left hand specimen is nr. 17077 (probably *P. rufolavatus*); the right hand specimen is nr. 17031 (*P. ruficollis*).

The other specimen is more irregularly and darker spotted on the sides of the head and neck, lacks the rufous patches and has the thinner, and longer bill of *P. rufolavatus* (nr. 17077; Plates V and VI). It probably represents the juvenile plumage of that species. However, in the place where it was collected, only one adult *P. ruficollis* was in the vicinity.

The remaining specimens are hard to identify with certainty. Together with the specimens mentioned above, they are tabulated in Tables 1 and 2. In most if not all of these specimens, the colour of the bill, or at least of the lower mandible, is light yellowish or flesh colour with darker spots. Most probably some of these specimens are intermediates of *rufolavatus* and *ruficollis*.

DISCUSSION OF CHARACTERS (Table 3)

Podiceps pelzelinii is a short-billed, long-winged, red-eyed grebe. Its body weight is lowest of the three, averaging 177 grams in four males and 145 grams in one female. It is noteworthy that when disturbed and

TABLE 1
NON-BREEDING AND IMMATURE *P. rufolavatus* AND *P. ruficollis*

Nr.	Sex	Date (1960)	Locality	Tentative Identification	Wing	Bill
17063 ¹⁾	♂	6.VII	Lake Alaotra (Vohimenakely)	<i>rufolavatus</i>	95	25
17041 ¹⁾	♂	30.V	Lake Alaotra (south)	<i>rufolavatus</i>	93	24
17036 ¹⁾	♀	24.V	Lake Alaotra (Andreba)	<i>rufolavatus</i>	90	23
17031 ²⁾	♂	20.V	Tananarive (Lake Lohazozoro)	<i>ruficollis</i>	98	20
17077 ²⁾	-	4.VI	Lake Alaotra (Ambatosoratra)	± <i>rufolavatus</i>	90	20
17054	♂	15.VI	Andilamena (Barrage of Ambadivato)	± <i>ruficollis</i>	—	22
17056	♂	15.VI	Andilamena (Barrage of Ambadivato)	± <i>rufolavatus</i>	—	22
17052	♀	15.VI	Andilamena (Barrage of Ambadivato)	<i>ruficollis</i>	98	—
17053	♀	15.VI	Andilamena (Barrage of Ambadivato)	<i>ruficollis</i>	93	19
17045	♀	30.V	Lake Alaotra (south)	± <i>rufolavatus</i>	87	23
17035	♀	24.V	Lake Alaotra (Andreba)	± <i>ruficollis</i>	100	19
17043	♀	30.V	Lake Alaotra (south)	± <i>rufolavatus</i>	90	21
17033	♀	24.V	Lake Alaotra (Andreba)	± <i>ruficollis</i>	96	21
17068	♂	7.VII	Lake Alaotra (Imerimandroso)	intermediate	94	22

¹⁾ See, Plate V.

²⁾ See, Plate VI.

TABLE 2

CHARACTERS OF NON-BREEDING AND IMMATURE *P. rufolavatus* AND *P. ruficollis*

Nr.	Colour of Bill	Colour of Iris	Plumage
17063	dark grey; lower mandible partly yellow with grey spots	light yellow, with some grey	like adult <i>rufolavatus</i> (Plate V)
17041	—	light	as above, with small dark spots on sides of head (Plate V)
17036	grey; lower mandible partly lighter	light yellow	as above, with more dark spots on sides of head (Plate V)
17031	flesh colour and yellow, darker on the culmen	brown	juvenile <i>ruficollis</i> (Plate VI)
17077	spotted grey and yellow	grey	probably juvenile <i>rufolavatus</i> (Plates V and VI)
17054	black, with light tip	brown	almost adult <i>ruficollis</i> ; but chin light grey, and sides of head greyish rufous
17056	dark, with light tip, and light underside of lower mandible	brown	like adult <i>rufolavatus</i> ; but chin mixed white and grey, and sides of head pale rufous
17052	yellow-flesh colour; culmen and base dark grey	brown	incomplete breeding plumage of <i>ruficollis</i>
17053	dark, irregularly spotted with light	brown	incomplete breeding plumage of <i>ruficollis</i> with light grey sides of neck
17045	in skin: dark, with mainly yellowish lower mandible	—	like probably juvenile <i>rufolavatus</i> ; but some pale brownish feathers on sides of neck
17035	grey, irregularly spotted with flesh colour	brown, with light brownish yellow outer circle	irregularly spotted head; could be juvenile <i>ruficollis</i>
17043	dark grey and flesh colour	light brown	sides of head irregularly spotted grey and dark brown; could be juvenile <i>rufolavatus</i>
17033	dark grey; base of lower mandible flesh colour	brown, with lighter outer circle	head spotted dark grey and pale rufous; could be juvenile <i>ruficollis</i>
17068	dark grey, base of lower mandible and part of upper mandible flesh colour	brown, outer circle lighter	head spotted; pale rufous reversed on nape; intermediate between juvenile <i>ruficollis</i> and <i>rufolavatus</i>

TABLE 3

CHARACTERS OF ADULT MADAGASCAR GREBES (*Podiceps*)

Species	Body-Weight		Tarsus and Middle Toe (average of males and females combined)	Bill	Wing	Chin	Colour of Iris
	Average of Males	Average of Females					
<i>pelzelnii</i>	177 g	145 g	80.5 mm	short	long	light grey	dark red
<i>rufolavatus</i>	199 g	186 g	80.7 mm	long	short	white or light buff	light yellow
<i>ruficollis</i>	207 g	176 g	79.8 mm	short	long	black	brown

chased these birds most frequently fled with flapping wings and feet over and above the water, whereas the other species fled by diving.

Podiceps rufolavatus is a long-billed, short-winged, yellow-eyed grebe. Its body weight is about that of *ruficollis*, being on average 199 grams in eight males, and 186 grams in five females.

Podiceps ruficollis is a short-billed, long-winged, brown-eyed grebe. Its body weight is about that of *rufolavatus*, being on average 207 grams in six males and 176 grams in six females.

It is noteworthy that the adult specimens considered as intermediates between *rufolavatus* and *ruficollis* on account of plumage characters, also fall in between these species when lengths of wing and bill are compared. Even the type specimen of the name *rufolavatus* (in the Paris museum) is intermediate in coloration (rufous sides of head; dark grey chin) and in proportions (long-billed; long-winged) (See, DELACOUR 1933, coloured plate opposite p. 4. See also, Fig. 1 and 2). A similar specimen collected by the Madagascar Expeditions and now in the New York museum (nr. 410436) has the sides of the head dark reddish brown like in *ruficollis* and the feathers of the chin suffused with grey; it is short-winged (92.5 mm), but unfortunately the bill is broken.

Those specimens in non-breeding plumage, which on account of plumage characters are hard to assign to either *rufolavatus* or *ruficollis*, likewise are intermediate in measurements. Of these, nr. 17068 is definitely intermediate, both in plumage characters and in the proportion of wing and bill.

The data presented above seem to provide sufficient evidence of the interbreeding of *P. rufolavatus* and *P. ruficollis*. At the same time they

do not seem to support DELACOUR's original assumption of the occurrence of two colour phases in *P. rufolavatus*. Instead, specimens in the darker phase of *rufolavatus* are according to this theory, hybrids of *rufolavatus* and *ruficollis*. The type specimen of *rufolavatus* must on the same grounds be considered a distant hybrid.

Another interesting situation appears when comparing the Madagascar specimens of *P. ruficollis* recently collected by Mrs. PAYNE with specimens from continental Africa. Differences in plumage could not be found, but instead, a tendency is apparent for Madagascar birds to have a longer bill and a shorter wing. This is most noteworthy in the four specimens collected on Lake Alaotra, where *P. ruficollis* occurs alongside with *P. rufolavatus* (Fig. 5 and 6). A longer bill and a shorter wing represent at the same time the proportional characters in which *P. rufolavatus* differs from the short-billed, and long-winged *P. pelzelinii*.

Careful study of 27 specimens of grebes collected by the Madagascar expedition under DELACOUR's direction, and preserved in the museums in Paris, London and New York showed that apart from the type specimen of *rufolavatus* mentioned above, and probably a similar specimen in the New York museum, perhaps two or three specimens in immature plumage show characters of *ruficollis* and therefore may probably be of hybrid *rufolavatus* x *ruficollis* origin. However, as the head pattern of juvenile Madagascar grebes are not sufficiently well known, we think we have to restrict ourselves to only mentioning these specimens below and leaving it to future students to work out the details of the plumages of downy young and immatures.

British Museum Reg. 1931.8.18.1132. ♀ imm. 7 June 1929, Andreba, Lake Alaotra. Probably *rufolavatus* x *ruficollis*; not *pelzelinii* as ultimately identified on the label (field label: "*ruficollis capensis*").

Paris Museum, Nr. 130. ♀ imm. 1 June 1929, Andreba, Lake Alaotra. Probably *rufolavatus* or *rufolavatus* x *ruficollis*; not *pelzelinii* as ultimately identified on the label.

Paris Museum, Nr. 129. ♀ imm. 8 June 1929, Andreba, Lake Alaotra. Probably immature *P. ruficollis*: some blackish on the sides of the head and some brownish on the occiput are remains of the immature plumage. Not *pelzelinii* as ultimately identified on the label (field label: "*ruficollis capensis*"). Wing $98\frac{1}{2}$; bill 20; tarsus $35\frac{1}{2}$; middle toe 46 mm.

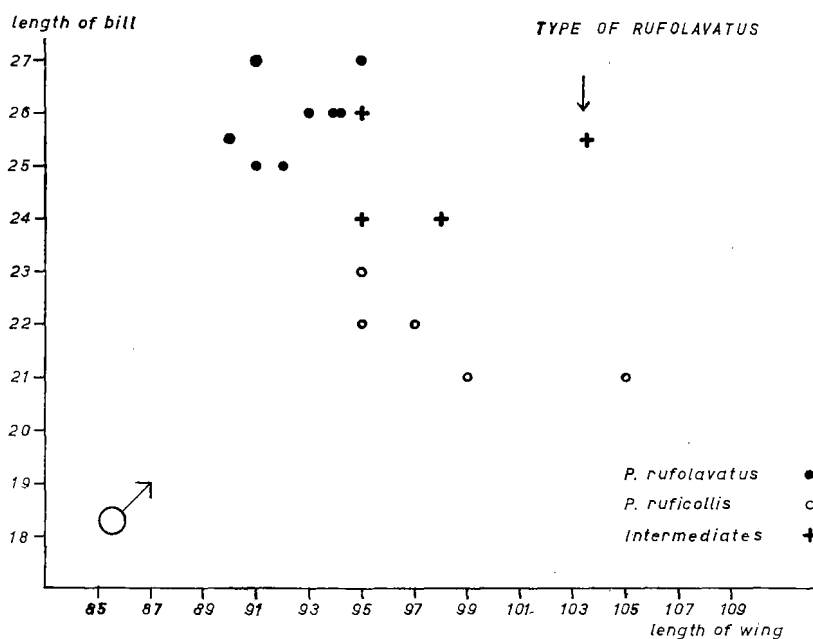


FIGURE 1. Length of bill in relation to length of wing in *Podiceps rufolavatus*, *P. ruficollis*, and presumed hybrids in Madagascar (males).

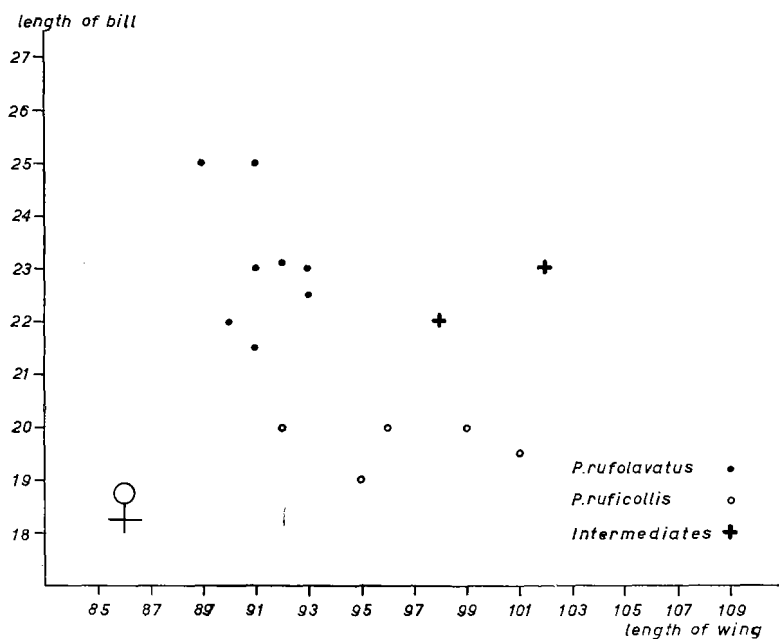


FIGURE 2. Length of bill in relation to length of wing in *Podiceps rufolavatus*, *P. ruficollis*, and presumed hybrids in Madagascar (females).

PRESENT DISTRIBUTION AND ECOLOGY

Podiceps pelzelinii is generally reported to be a common breeding bird in Madagascar (RAND 1936). However, in 1960, Mrs. PAYNE saw less than 10 specimens, in Lake Alaotra and around Andilamena only. Five specimens were collected. It was definitely the rarest of the grebes.

The stomach contents of the specimens collected contained feathers (4×), fish (2×), insects (2×, in one instance aquatic Heteroptera), crustaceans (1×). No differences in habitat with the other species could be established, but probably *pelzelinii* is less definitely a fish-eater than *rufolavatus* and *ruficollis* in Madagascar.

Podiceps rufolavatus was observed in Lake Alaotra only, where Mrs. PAYNE estimated the total number seen at fifty; 13 specimens attributed to this species were collected. The collecting was not done at random, as more attention was paid to light-headed individuals than to the darker ones, which at first were thought by Mrs. PAYNE to be *ruficollis*. Therefore the proportion of intermediate specimens must be higher than indicated by the number of the specimens collected.

In the museum in the *Palais de la Reine* at Tananarive Mrs. PAYNE examined a mounted, un-sexed specimen of this species said to originate from Miarinarivo, a locality which is hard to locate, as several small villages in Madagascar are known bearing this name.

The stomach contents were almost exclusively the remains of fish (see Table 4).

Podiceps ruficollis, although not recorded or collected by HARTLAUB (1861) and RAND (1936), but recorded by MILON (1946) in large numbers from Lake Anosy (see previous chapter), was the commonest of the grebes in Madagascar during Mrs. PAYNE's visit in 1960. It was seen in all regions visited. At least 13 specimens were collected in the following localities: around Tananarive (6, viz. Lake Mandroseza, Imerimanjaka marsh, Lake Lohazozoro, small lake near Lake Mantasoa, and Lake Itasy), Lake Alaotra (4, viz. near the villages Andreba, Andromba, and Ambahitsaratany), Andilamena (3, artificial lake at Ambadivato).

The stomach contents did not differ from those of *P. rufolavatus* and showed more fish than the stomachs of 20 birds previously collected by Mrs. PAYNE in South Africa (Hoopvlei, Western Cape Province). The dominance of fish in the grebes' diet is apparent from Table 4. Small fish, of less than 5 cm length (mainly *Tilapia*) were abundant in all lakes and marshes in Madagascar where grebes were found. In the fresh

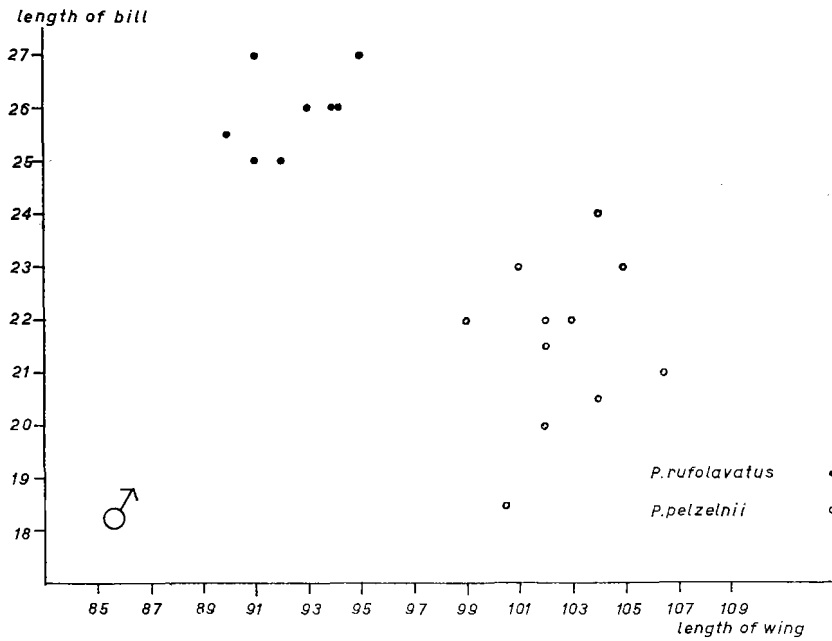


FIGURE 3. Length of bill in relation to length of wing in *Podiceps rufolavatus* and *P. pelzelinii* (males).

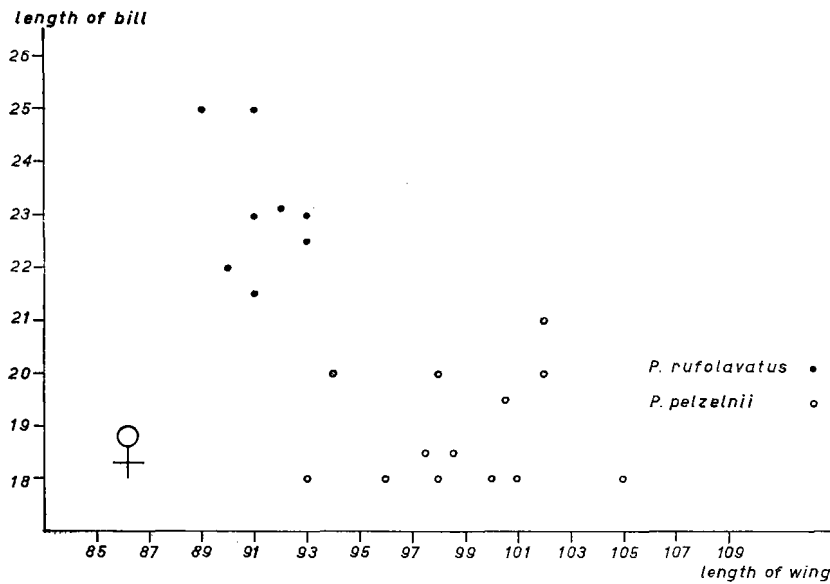


FIGURE 4. Length of bill in relation to length of wing in *Podiceps rufolavatus* and *P. pelzelinii* (females).

STOMACH CONTENTS OF *M.*
(*P. rufolavatus*)

	Number of specimens	Feathers		
		numerous	few	absen
Lake Alaotra, Madagascar	28	8	11	9
Hoopvlei, South Africa	20	0	8	12

water areas of Hoopvlei, South Africa, however, insect larvae (a.o. Odonata) were far more numerous. Table 4 also shows that a fish diet corresponds with the presence of numerous feathers in the stomach. The table clearly suggests that these grebes consume more, and more regularly feathers when eating fish than when mainly subsisting on insects. The ball of feathers probably prevents the sharper fish bones from entering the intestines before these have been dissolved by the stomach secretions.

Apart from seven suspected and possible hybrids (Table 2), five adult and one immature hybrid specimens have been collected in Lake Alaotra. No definite indications of mixed pairs or pair formation have been observed, but Mrs. PAYNE frequently observed birds of different species occurring in mixed flocks.

No eggs and only one downy chick was found in the period 1 May-27 July, and only a few times two birds were seen in a kind of courtship. On 6 July one of the birds performing the "duet-ceremony" was collected and proved to be a male with intermediate plumage (nr. 17064), its testes being of fair, though not exceptionally large size (left one 8×5 , right one 6×4 mm). The average size of the testes of the collected males was found to be as follows (*P. rufolavatus* and *P. ruficollis* combined; juvenile birds not included).

May (6 specimens): left 8.2×5.1 mm, right 6.7×4.1 mm
 June (4 specimens): left 8.2×5.2 mm, right 7.2×4.0 mm
 July (5 specimens): left 8.4×4.4 mm, right 7.0×3.8 mm

Mrs. PAYNE considered that, at all events during the season prior to her visit, courtship and pair formation had taken place in December, followed by the main breeding activity in the months of January to March.

4

AND SOUTH AFRICAN GREBES
(*ruficollis* COMBINED)

Fish			Insects		
numerous	few	absent	numerous	few	absent
15 0	6 0	7 20	1 4	3 9	24 7

GEOGRAPHICAL ORIGIN AND SPECIES FORMATION

It is tempting to speculate on the geographical origin and the species formation of the Madagascar grebes.

P. pelzelinii is considered the oldest of the present species of small grebes in Madagascar, on account of its colour pattern, which is different from that of any of the small grebes and which in some way is resembling that of the large, holarctic *P. griseigena*. It is beyond the scope of this paper to speculate about the origin and the time and the way in which *pelzelinii* has settled in Madagascar.

P. rufolavatus, then, is the next oldest species. Since it is apparently capable of interbreeding with *P. ruficollis*, it has to be considered as conspecific with it. It is likely that *rufolavatus* has arisen from the main Old World *ruficollis*-stem. Presumably it has colonized Madagascar from continental Africa and it is thought to have acquired its present characters by geographic, insular, isolation in Madagascar. Being of about equal size, *pelzelinii* and *rufolavatus* have, in accordance with GAUSE's principle, diverged into slightly different ecological directions. *Pelzelinii* has evolved into a short-billed, long-winged species (more "movable" and more widely spread; less exclusively a fish-eater); *rufolavatus* has evolved into a long-billed, short-winged form (more sedentary, with a more restricted area; more exclusively a fish-eater). See, Fig. 3 and 4. Its restricted occurrence in Lake Alaotra makes it a most vulnerable form.

P. ruficollis apparently has spread over Madagascar only in the last twenty or thirty years, at least from 1945 onwards (MILON 1946). It is clearly a recent colonist from continental Africa. It is now merging on Lake Alaotra with *rufolavatus*, which it apparently still recognizes as a breeding partner. Its structural characters are more or less in between those of *pelzelinii* and *rufolavatus*; hence it is probably disturbing the

ecological balance between these species. In comparison to the present continental African population (*P.r. capensis*), the Madagascar population seems to be on its way to acquiring a longer bill. It would be interesting to know whether this is the result of hybridization with *P. rufolavatus* (which has a long bill), or whether the long bill is acquired under the stress of competition with the indigenous *P. pelzelinii* (which has a short bill), thus, repeating the evolution of present *P. rufolavatus*. It may also be the result of both, though on Lake Alaotra it is most likely to be caused by hybridization. So far, intermediates between *rufolavatus* and *ruficollis* have only been recorded from Lake Alaotra. See, Fig. 1-6.

It seems evident that *P. pelzelinii* has considerably decreased in numbers. As the structural characters of the invading *ruficollis* more closely resemble *pelzelinii* than *rufolavatus*, it is not likely that the decline of *pelzelinii* is caused by the recent colonisation of *P. ruficollis*. The structure and present ecology of these species make it not improbable that the decline will continue.

It is equally evident that *P. ruficollis*, in interbreeding with *P. rufolavatus*, is "swallowing up" the small population supply of that form. It is most likely that in the near future the characters of a hybrid population *rufolavatus* \times *ruficollis* on Lake Alaotra will become more stabilised, probably in the direction of a longer billed and shorter winged type than present *ruficollis* (*capensis*). If this process actually is proceeding on the same scale as reported in 1960 the *rufolavatus* type of grebe seems to be doomed to vanish.

NOMENCLATURE

From the fact that the type specimen of the name *Podiceps rufolavatus* DELACOUR, 1932, preserved in the Paris Museum, possesses characters suggesting hybridization of light-headed "*rufolavatus*" and rufous-headed *ruficollis*, a nomenclatorial question unfortunately arises, which, however, is beyond the scope of scientific interest. When the process of merging of *P. "rufolavatus"* and *P. ruficollis capensis* proceeds as indicated in the previous chapter, either the new hybrid population, or, more likely, the old, light-headed, yellow-eyed, long-billed indigenous population will deserve a new name. The group in this paper currently named "*rufolavatus*", then, apparently has a subspecific rather than a specific value and should be named *Podiceps ruficollis rufolavatus* DELACOUR. The name remains applicable to the population of Madagascar dabchicks evolving at present, whether this is of a hybrid nature or not.

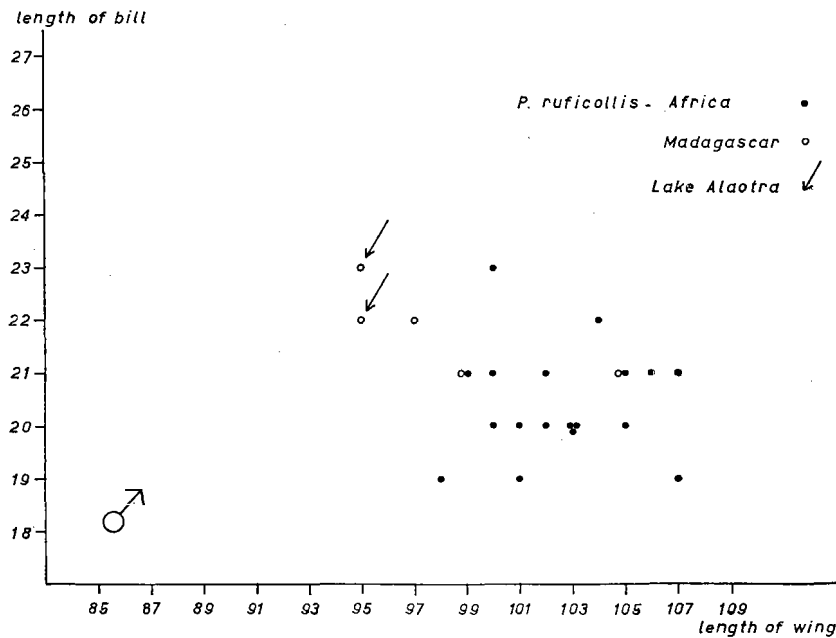


FIGURE 5. Length of bill in relation to length of wing in *Podiceps ruficollis* from continental Africa and from Madagascar (males); those originating from Lake Alaotra have been indicated by arrows.

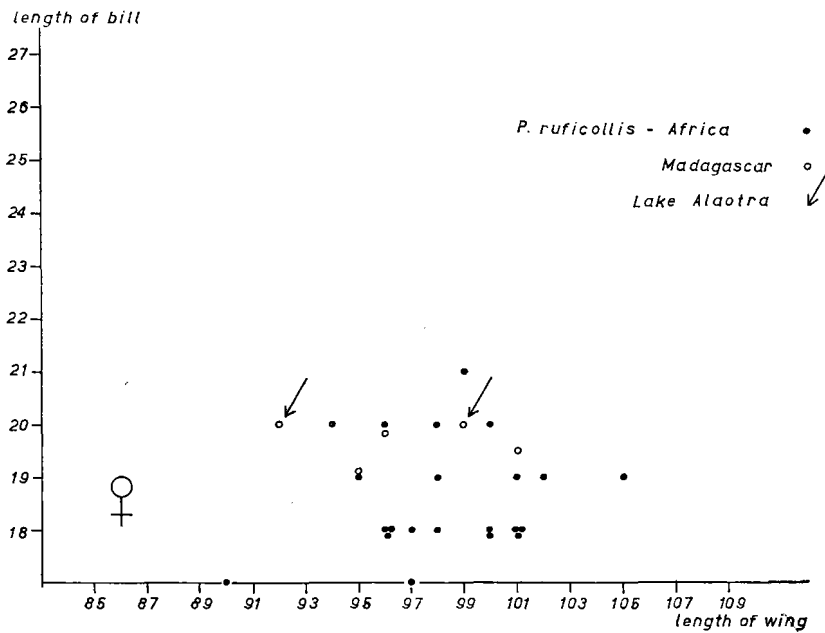


FIGURE 6. Length of bill in relation to length of wing in *Podiceps ruficollis* from continental Africa and from Madagascar (females); those originating from Lake Alaotra have been indicated by arrows.

SUMMARY

Three species of small grebes or dabchicks are reported from Madagascar. Two of these are endemic breeding birds: *Podiceps pelzelinii* and *P. rufolavatus*. The first of these species was described by HARTLAUB as early as 1861 and is generally recorded as common throughout the island in suitable fresh water localities. The second species was described by DELACOUR as late as 1932; it is only known from Lake Alaotra. A third species, *P. ruficollis* (African race *capensis*), was for many years considered as rare in Madagascar, where it was not known as a breeding bird. DELACOUR (1933) could only list 5 stray specimens in old collections. In 1945 MILON (1946) found it numerous on Lake Anosy near Tananarive.

The occurrence of more than one species of small grebe of almost similar size and proportions in one island presents problems of systematic, zoogeographic and ecologic interest. Therefore, Mrs. H. A. W. PAYNE visited Madagascar in May-July 1960, where she collected 44 specimens of grebes of all three species, in addition to distributional and ecological data.

P. pelzelinii was found to be the rarest of the grebes. At least five times as many *P. rufolavatus* were seen as *pelzelinii*. *P. ruficollis* was by far the commonest species. On account of juvenile birds collected, which apparently had been unable to make long flights, *P. ruficollis* was considered to have nested in Madagascar. The presence of intermediate specimens of *ruficollis* and *rufolavatus* in the series collected on Lake Alaotra was considered to provide sufficient evidence for a theory of hybridization of these species. All three species occurred alongside each other at Lake Alaotra, and apparently also had nested there.

Differences in proportions of length of bill and wing indicate that *pelzelinii* and *rufolavatus* are ecologically slightly distinct: *P. pelzelinii* being a long-winged, short-billed species, *P. rufolavatus* being short-winged and long-billed. *P. ruficollis* is in between; it therefore seems to be in a position to disturb the ecological balance between the two first named species. In comparison to continental *ruficollis* it has, however, on the average a longer bill, which it may have acquired in Madagascar, either through hybridization with *rufolavatus* or through competition with *pelzelinii*.

Mrs. PAYNE collected specimens intermediate between *rufolavatus* and *ruficollis* in various stages of plumage. Examination in the Paris Museum showed that in some characters the type specimen of *rufolavatus* is also intermediate with *ruficollis* and therefore probably is a distant hybrid. It also appeared that the material collected by the French-British-American expeditions to Madagascar under DELACOUR's direction contained one immature *ruficollis* and two or three specimens of supposed hybrid origin. So far, all intermediate specimens known originate from Lake Alaotra.

A theory is developed on the origin of the species of grebes at present breeding in Madagascar, and a tentative prognosis is given of the future development of this unique situation. Probably the oldest species is *pelzelinii*. It is expected to have a hard time to maintain itself against a spreading population of *ruficollis*. The next oldest species is *P. rufolavatus*, which is thought to have acquired its present, striking characteristics during a long period

of insular isolation of colonists of an old, African *ruficollis*-stem. *P. ruficollis* is the most recent African colonizer, probably from this century. It is now spreading rapidly throughout Madagascar, where it may have found favourable opportunities in connection with the destruction of original habitats and the presence of permanent artificial water reservoirs. In view of the supposed hybridization of *P. ruficollis* with *P. rufolavatus* on Lake Alaotra the authors fear that the present form *rufolavatus* will ultimately become merged into a stabilised hybrid population. The latter, as well as the present polymorphic population, will remain to be known as *P. ruficollis rufolavatus*. The original, long-billed, light-headed, yellow-eyed "*rufolavatus*"-population will in that case be in need of a new name.

SAMENVATTING

Op Madagascar komen drie soorten kleine futen of dodaarzen voor. Twee van deze zijn endemische broedvogelsoorten, dat wil zeggen, dat zij buiten Madagascar niet voorkomen. Het zijn *Podiceps pelzelni* en *P. rufolavatus*. De eerstgenoemde soort werd reeds in 1861 door HARTLAUB beschreven; hij wordt in het algemeen als een gewone verschijning beschouwd in alle geschikte zoetwaterbiotopen van het gehele eiland. De tweede soort werd pas in 1932 door DELACOUR ontdekt en beschreven; hij is alleen bekend van het Alaotra Meer. Een derde soort, de Dodaars, *P. ruficollis* (in het Afrikaanse ras *capensis*), werd tot voor kort als nog zeldzamer beschouwd en werd in tegenstelling tot de vorige niet als broedvogel van Madagascar genoemd. DELACOUR (1933) kon niet meer dan 5 exemplaren uit Madagascar achterhalen, merendeels afkomstig uit oude collecties. Pas in 1945 trof MILON (1946) de Dodaars talrijk aan op het Anosy Meer bij Tananarive.

Het voorkomen van meer dan één soort dodaars van vrijwel gelijke grootte en lichaamsproporties op één eiland, houdt belangwekkende problemen in van systematische, zoögeographische en oecologische aard. Uit dit oogpunt bezocht Mevrouw H. A. W. PAYNE-SMIT, destijds assistente bij het Zoölogisch Museum van de Universiteit van Amsterdam, Madagascar van mei tot juli 1960. In die tijd verzamelde zij 44 exemplaren van de bovengenoemde drie soorten futen, terwijl zij voorts gegevens over hun verspreiding en oecologie bijeenbracht. De verzamelde exemplaren bevinden zich thans in het Zoölogisch Museum te Amsterdam.

P. pelzelni was de zeldzaamste soort. Mevr. PAYNE zag minstens vijf maal zo veel *P. rufolavatus* dan *P. pelzelni*. Daarentegen vond zij *P. ruficollis* verreweg de talrijkste van de dodaars-soorten op Madagascar. Op grond van door haar verzamelde jonge vogels, die klaarblijkelijk nog te klein waren om grote vluchten te hebben kunnen uitvoeren, zijn de auteurs tot de overtuiging gekomen, dat *P. ruficollis* wel op Madagascar moet broeden. Mevr. PAYNE verzamelde exemplaren van alle drie soorten op het Alaotra Meer en nam aan, dat deze daar ook alle drie gebroed hadden. In de op het Alaotra Meer bijeen gebrachte serie bevinden zich ook exemplaren die in morphologische kenmerken het midden houden tussen *ruficollis* en *rufolavatus*. Deze intermediaire exemplaren worden door de auteurs als directe of indirecte bastaarden tussen *ruficollis* en *rufolavatus* beschouwd. Deze vondst heeft belangwekkende consequenties op het punt van de systematiek en de herkomst van de vorm *P.*

rufolavatus. Hij zou als een Madagassisch eilandras van de Dodaars, *Podiceps ruficollis*, moeten worden beschouwd.

Omdat de lengte-verhoudingen van snavel en poten bij *pelzelinii* en *rufolavatus* verschillend zijn, nemen de auteurs aan, dat tussen deze soorten geringe oecologische verschillen bestaan: *P. pelzelinii* is namelijk een langvleugelige en kortsnavelige soort, *P. rufolavatus* daarentegen is kortvleugelig en langsnavelig. *P. ruficollis* staat hier tussen in en schijnt daardoor in staat te zijn het oecologische evenwicht tussen de twee eerst genoemde soorten te verstoren. In vergelijking met continentaal Afrikaanse Dodaarzen heeft *P. ruficollis* van Madagascar naar verhouding een langere snavel; deze situatie zou zowel door bastaardering met de langsnavelige *rufolavatus*, als door soort-concurrentie met *pelzelinii* kunnen zijn ontstaan.

De door Mevr. PAYNE verzamelde intermediaire exemplaren tussen *rufolavatus* en *ruficollis* hebben betrekking op vogels in volwassen, zowel als in onvolwassen verenkladden. Het bleek, dat ook het in het Natuurhistorisch Museum van Parijs bewaarde type-exemplaar van de naam *P. rufolavatus* in enkele kenmerken intermediair is met *ruficollis* en dus een mogelijke indirecte bastaard is. Ook het materiaal dat onder DELACOURS leiding door de Frans-Britse-Amerikaanse expedities naar Madagascar werd verzameld en dat zich thans verspreid in de musea te Parijs, Londen en New York bevindt, en door de auteurs bestudeerd kon worden, bleek minstens twee of drie exemplaren te bevatten, die als mogelijke bastaarden kunnen worden beschouwd. Tot heden zijn dergelijke intermediaire exemplaren alleen nog maar op het Alaotra Meer verzameld.

Op grond van deze gegevens hebben de auteurs een theorie over de oorsprong van de drie soorten futen op Madagascar opgebouwd en hebben zij het gewaagd een voorzichtige blik vooruit te werpen op de ontwikkeling die zij van deze uit theoretische overwegingen wel als uniek te beschouwen situatie verwachten. *P. pelzelinii* wordt door hen als de oudste soort beschouwd. De auteurs verwachten dat hij het in de toekomst waarschijnlijk erg moeilijk zal krijgen om zich tegen de zich snel uitbreidende Afrikaanse Dodaars, *P. ruficollis*, te handhaven. *P. rufolavatus* is de op een na oudste vorm op Madagascar. Hij heeft zich waarschijnlijk door langdurige isolatie op Madagascar uit een oude *P. ruficollis*-stam ontwikkeld. Ondanks zijn vergevorderde morphologische differentiatie blijkt hij de in recente tijd Madagascar opnieuw gekoloniseerde *P. ruficollis* nog als voortplantingspartner te herkennen. Op het Alaotra Meer hebben deze vormen een polymorphe broedpopulatie doen ontstaan. Naar het oordeel van de auteurs heeft deze een grote kans zich tot een meer stabiele intermediaire populatie te ontwikkelen, waarin dan de oorspronkelijke "*rufolavatus*" geheel zal zijn opgegaan. Deze populatie zal de naam *P. ruficollis rufolavatus* moeten blijven dragen. Als dit allemaal zo zal plaats vinden, zal daarentegen de oorspronkelijke, dan wel verdwenen, "*rufolavatus*" met zijn lange snavel, lichte kop en gele ogen een nieuwe naam nodig hebben.

REFERENCES

- DELACOUR, J. 1932. Les oiseaux de la mission zoologique franco-anglo-américaine à Madagascar (1929-1931). Ois. Rev. Fr. Orn. 2: 6.
- DELACOUR, J. 1933. Les grèbes de Madagascar. Ois. Rev. Fr. Orn. 3: 4-7.
- MILON, Ph. 1946. Observations sur quelques oiseaux de Madagascar. Ois. Rev. Fr. Orn. 16: 82-86.
- RAND, A. L. 1936. The distribution and habits of Madagascar birds. Bull. Am. Mus. Nat. Hist. 72: 143-499.