ONTOGENY OF BEHAVIOUR IN FIVE SPECIES OF GREBES

by

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PUBLICATIONS

Courtship, hostile behavior, nest-establishment and egg-laying in the Eared Grebe (*Podiceps caspicus*). Auk, 75: 290-311. 1958.

Copulation in the Pied-billed Grebe. N. M. McAllister and R. W. Storer, Wilson Bull. in press. 1963.

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of

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COMMITTEE IN CHARGE

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ONTOGENY OF BEHAVIOUR IN FIVE SPECIES OF GREBES

ABSTRACT

The resting postures, locomotion, feeding behavior, and comfort movements of five species of grebes (Podiceps caspicus, P. auritus, P. grisegena, Podilymbus podiceps, and Aechmophorus occidentalis) are described, compared, and their development traced to the adult form. Each pattern is then compared with its counterpart in other groups of birds, and its adaptive significance is considered. In defecation, climbing-up, and begging the eliciting stimuli are examined.

The stages of development are traced, and it is found that the birds hatch at the beginning of stage two, the first appearance of comfort movements. They pass into stage three, the maturation of comfort movements, within a few hours and remain in this stage until the adult sleep posture is assumed, functional preening and oiling are established, and spontaneous swimming appears, at eight days. Stage four includes the appearance of simple bathing, diving, and the substitution of following for riding on the parent's back. Stage five, beginning about the sixteenth day includes matured bathing, alarm, self-feeding, and finally flight.

Because of the great increase in length of stage three over that of precocial birds, the inability of the chicks to maintain the adult sleep posture, the lack of functional preening and oiling, and the depression of all activity, it is suggested that the grebes be considered not precocial birds but semi-precocial birds with the gulls. They are adapted by these attributes and by the controlled defecation response to life in a nest. The grebe nest being unsuitable for prolonged brooding, the grebe broods its chicks on its back.

GRADUATE STUDIES

Field of Study: Zoology

Comparative Ethology	M.D.F. Udvardy W.S. Hoar
Biology of Galliform Birds	J. Bendell
Ornithology	R.W. Storer
Birds of the World	R.W. Storer
Evolutionary Mechanics	T.H. Hubbell

Other Studies:

Advanced Animal Nutrition	A.J. Wood
Psychology of School Subjects	N.V. Scarfe
Theories and Principles of Educational Administration	D.C. Smith

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TABLE OF CONTENTS

INTRODUCTION

The ontogeny of resting, locomotion, comfort movements and feeding behaviour in grebes has been traced. Each pattern is described as it first appears and as it develops into the adult form. The adaptation of the behaviour to the environment is considered, and the eliciting stimuli are examined. Comparisons are made with the development of other groups, particularly with those precocial birds which are also adapted to maturing in an aquatic environment.

Grebes have been placed (Nice 1962) with loons and rails in a precocial IV grouping, birds whose young are led by the parent and fed by it. The grebes were described as being a very aberrant group as they ride the parent's back instead of following. But it is the object of this study to examine the concept that grebes may be, with the gulls, semi-precocial birds, birds whose young stay at the nest though able to walk. The behaviour of young grebes is, like semi-precocial birds, slow in developing through stages three and four, and adapted to life in a restricted space which they do not leave voluntarily. The "nest" of the downy grebe is its parent's back.

Problem: Upon hatching, young grebes have the eyes open. They are active, able to climb, swim, beg, eat, and stretch within an hour after emerging from the egg. But temperature regulation is very poor, and the down is not waterproof. Until the feathers resist wetting and temperature can be maintained, the chick is brooded constantly. Since the nest is wet and subject to flooding from changes in water level, the grebe broods the young on its back. In sleep the chick sprawls with the head out on the substrate, a posture

unsuited to resting on the water, and young grebes sleep most of the time. Preening, shaking, and bathing movements are not functional. In order to remain on the parent's back, the downy must have well-developed overtaking and climbing responses. Defecation is controlled so that the young do not defecate on the parent's back. Begging is well-developed. The following and alarm responses of precocial young are not necessary and are absent.

As the second down begins to develop, and the young bird can spend some time on the water, it gradually develops the resting and sleep postures of the adult, takes over the care of its plumage, and discontinues climbing movements in favour of following. Then it begins to feed itself and loses the begging and following responses.

Literature: The ontogeny of behaviour is relatively well known in several orders of birds. Nice (1943) has studied behaviour of young Song Sparrows and other passerines. Tinbergen and his students have made many studies on development of gulls, especially their begging patterns. Van Iersel and others have studied the young of terns. A number of people have worked with ducklings, especially on imprinting and following. The most exhaustive of these studies is that of Fabricius (1951). Olson and Marshall (1952) and Beebe (1907) give some observations on behaviour of young loons. Heinroth (1928) has photographs of the feather development of the Great Crested Grebe and the Little Grebe, descriptions of swimming and feeding, but no descriptions of the behaviour of the young. Nice (1962) has brought together observations on the development of precocial groups to show that they all fit into the same sequential pattern as that exhibited by altricial young. The first quiescent stage is, in precocial birds, passed within the egg, and the second stage of first appearance of comfort movements takes only a few hours. The maturation of comfort movements, stage 3, takes about a day, and then the

young enter a locomotory stage where they leave the nest but are still dependent on the adults. The final stage begins with use of aggression and includes socialization and perfection of self-feeding.

The development of behaviour in grebes has been almost completely neglected. Simmons (1955) has a very incomplete section on the young of the Great Crested Grebe (Podiceps cristatus) in the wild, and other accounts of wild grebes include only a few short notes on frequency of feeding by the adults. Mrs. Nice and the Heinroths both attempted to raise grebes from hatching and were successful only in keeping them alive a few days. The observations of Nice (1962) cover only the first few hours, well into stage two, i. e. the first appearance of comfort movements.

The non-reproductive behaviour of adult grebes is also very poorly documented. There are in the literature three reports on captive adult Horned Grebes (Dubois 1918, Aldrich 1929, Woolfenden 1956) and two on captive Red-necked Grebes (White 1931, Shelley 1930). These, while short, are valuable and have been referred to where pertinent. No descriptions of the non-reproductive behaviour of the Pied-billed or Eared Grebes are available. Lawrence (1950) has studied the diving of the Western Grebe, and Wetmore (1924) examined the stomach contents of the North American species for feeding habits and feather eating. Simmons (1956), Storer (1961) and others examined the functions of feather eating. In Simmons' (1955) paper on the Great Crested Grebe there are a few observations on comfort movements.

The non-reproductive behaviour of other non-passerine groups is also largely unstudied. McKinney's (M. S.) monograph on the comfort movements of the Anatidae has been exceedingly useful for comparison. Nice (1943) includes descriptions of the comfort movements of passerines which have also been used.

METHODS

The five species studied were the Eared Grebe (Podiceps caspicus), the Horned Grebe (Podiceps auritus), the Red-necked Grebe (Podiceps grisegena), the Pied-billed Grebe (Podilymbus podiceps), and the Western Grebe (Aechmophorus occidentalis).

The standard for the descriptions of adult and juvenal behaviour consisted of numerous field observations of Eared, Pied-billed and Red-necked Grebes. It was necessary to bring the birds into the laboratory to obtain precise descriptions of the behaviour patterns, ages at appearance and changes in frequency of use, and to perform experiments on eliciting stimuli. Lorenz has said that the best way to observe the reactions of a young animal to its parent is to be that parent yourself. Reactions to the observer help in ascertaining the stimulus situations for certain actions and their functional value.

During the summer of 1958 at Ann Arbor, Michigan, three young Pied-billed Grebes were studied under laboratory conditions. Each was captured when only a few hours old. One died when three days old, one at seven days. The third was released in excellent condition at forty-five days. At the same time three wild siblings of these birds were under observation. Physical and behavioural development were the same in wild and captive birds.

The captive young were kept in a cardboard box with a lamp over it for warmth during the day and an electric heating pad in the bottom at night. The flooring in the box was of absorbent cloth, since the droppings were wet and tended to foul the feathers. Later the remaining bird was moved to an outdoor cage with newspaper flooring. In the outdoor cage no heat source was needed.

The birds were fed by hand at one to two hour intervals from 6 A. M. to 10 P. M. Food was caught locally with seines and given fresh where possible.

When this was not possible, the food was frozen and then defrosted under warm water before being used. The bulk of the food consisted of whole fish one to six inches long. These included various species of sunfish and minnows and the mud minnow Umbra limmi. The remainder consisted of crayfish and dragonfly larvae.

Photographs were taken with 16 mm. movie camera and a four inch lens. Drawings for study and illustration were made from these films by projection.

At the Waterfowl Research Station at Delta, Manitoba, during June and July 1961, eighty eggs of four species were collected in small groups in the marsh and incubated in the duck hatchery on the station. 78 of the 80 eggs hatched. Mortality of the chicks is discussed in the text where applicable. The ages to which the birds were raised is shown in Table I.

Table I. Chicks Studied

Species	No.	Age at death or release	Place and date of capture
Pied-billed	1	3 days +	Ann Arbor 1958
	1	7 +	Ann Arbor 1958
	1	45 r	Ann Arbor 1958
	11	2-5 +	Delta 1961
	2	10 +	Delta 1961
	1	7 +	Delta 1961
	1	6 +	Delta 1961
Eared	1	24 +	Delta 1961
	5	2-5 +	Delta 1961
Red-necked	1	9 +	Delta 1961
	1	6 +	Delta 1961
	11	2-5 +	Delta 1961
Western	13	2-5 +	Delta 1961
	1	10 +	Delta 1963
	1	8 +	Delta 1963
	6	3 +	Delta 1963
	8	2 +	Delta 1963
	2	6 alive	Delta 1963
Horned	1	7 +	Delta 1963

Continuous observations were made from four to six hours every day, with supplementary spot checks at other times during the day. Notes were taken in paragraphs of description with continual checking for variation. Then later, typical two hour stretches of the behaviour of single individuals were tabled and every movement included. These served to check the extent of individual variation and the number of movements involved at various ages.

Standard infra red lamp housing for ducks was tried, but the birds did better in the damp even heat of the incubator room with electric heating pads as a local source of warmth. Food, given by hand at one to two hour intervals, included fish, beef strips, minced beef, and turkey starter mash and is discussed further under begging and feeding. Water was available in shallow dishes or pans, and some of the birds were allowed to bathe regularly a number of times a day in a bucket or tub.

In June 1963, 18 Western Grebe eggs and 1 Horned Grebe eggs were air shipped from Delta, Manitoba, and hatched in a portable still air incubator. They were maintained by the same methods used in the later part of the 1961 season. These observations have not been completed at the time of writing, but one Western Grebe has reached eight days, and one ten, four have reached three days, six died younger, one Horned Grebe has reached 7 days. These birds have been used for experiments on the stimuli involved in defecation and climbing as well as in further observations on development.

For comparison with the behaviour of the young birds one adult Pied-billed Grebe was observed in captivity from March 23 until June 4, 1960. It was in full breeding plumage and remained in good health throughout the period of captivity. This bird was kept in a large tub during the day with a platform at water level. The water was changed every three hours at first,

but later it was found that changing it once during the day was sufficient to keep the bird's feathers in excellent condition. The grebe was moved to a box with sand in the bottom for the night to avoid fouling the water and its feathers. Sand was found to be a satisfactory material for the bottom of the box, as it absorbed the almost liquid droppings very quickly. The bird was fed frozen smelt, the only small fish available, about every two hours. It behaved normally in captivity.

An adult Red-necked Grebe was kept a similar length of time in 1955, but it was badly oiled and had to be kept out of water.

Each separate behaviour pattern is treated in the text under the headings description, occurrence, species variation, development, phylogenetic comparison, and adaptive correlates. The times cited are taken from movie film as are all the figures. Comparisons between behaviour patterns are made in tables where pertinent. Most patterns were observed hundreds of times in all species. In the few instances where observations were limited or where the behaviour was not studied in all species, this is noted in the text.

OBSERVATIONS OF WILD BIRDS

Problem: Observations of wild grebe chicks of known age serve to put into focus the behaviour seen in the laboratory. Does the decrease in climbing reactions coincide with the end of riding on the parent's back? How long after the beginning of spontaneous diving are the chicks fed by the parent? At what age are they independent, and then abandoned? At what age do they first fly? Unfortunately wild observations are exceedingly hard to obtain. The nest studied must be an isolated one, to avoid confusion with other birds, and most grebe nests are in colonies or several to a small pond. When leading young, grebes are secretive and keep within the reeds. They usually avoid the nest, and hours of time in blinds is rewarded by only a glimpse or nothing.

Timing of behaviour changes: For comparisons between species see Table II.

Pied-billed Grebe: One family of Pied-billed Grebes was followed until independent, and two siblings of these birds were kept in the laboratory for comparison. These birds were continuously on the back of the parent at four and five days respectively and the parent spent several hours resting on the now-flattened nest and on a muskrat house nearby. When the young were eleven and twelve days old, they followed about ten feet behind the adult for an hour and ten minutes, rode on the parent's back twenty-five minutes, and then spent an hour resting in shallow water while the adult fed alone.

By the seventeenth and eighteenth days the young were diving frequently but catching little, and they were not brooded. They had been abandoned between the twenty-sixth and twenty-eighth days. No attempts to fly were seen.

Red-necked Grebe: One family of six Red-necked Grebe chicks was followed for three weeks. On the seventh and eighth days of life, the chicks, which hatched on two successive days, were carried continuously by one or both parents and fed fish up to two inches long. On the twelfth and thirteenth days four young were seen, two carried and two following, and they were fed fish up to three inches long. On the twentieth and twenty-first days all but the youngest were following in the water and made no attempt to climb up. They were still being fed. Munro (1941) said that young were still with the parent at 29 days.

Eared Grebe: Eared Grebes in Holland were reported to be diving for food at two weeks, and fully independent at three weeks (Van Ijzendoorn in Nice 1962). Witherby (1943) said that they were expert divers at 17 days, but were still in the charge of the parents.

Great Crested Grebe: Hanzak (1952) stated that the first diving for food occurred at twenty days, and the young still attempted to climb onto the parent's back at four weeks. Simmons (1955) said that the chicks climbed on the parent's back "even when quite large, and I once saw a 15-day-old one squatting ridiculously on the adult's back." Both parents hunted food from the time that young were two weeks old. The chicks were fed to six or seven weeks and then were usually independent, though they could stay with the parents and be fed until 12 weeks.

Least Grebe: Gross (1949) said that Least Grebes (Podiceps dominicus) fed young three weeks old. They were fed on the parent's back for three days, after that they were fed in the water. On warm water these birds can apparently afford to be on the water sooner than more northern species.

They probably must be brooded most of the time to keep them dry.

Dabchick: Buddle (1939) reported that New Zealand Dabchicks (Podiceps rufopectus) fed young about three weeks old.

Little Grebe: Ashby (1933) reported that at two weeks the chicks (Podiceps ruficollis) were feeding themselves but brooded at night. Adults drove young away when the second clutch was started.

Western and Horned Grebes: No information available.

Table II. Development of Behaviour of Wild Grebes

Behaviour	Pied-bill	Red-neck	Eared	Dabchick	Great Crest	Least	Little
On parent's back:							
Continuously	0–7d	0–8d	-	-	-	0–4d	-
Intermittently	7–16d	12,13,20d	-	-	15d, 4w	-	2w
Diving for food	16d	-	17d	-	20d	-	2w
Fed but not carried	16–24d	21,29d	2w	3w	2w	3w	-
Independent	26–27d	-	3w	-	6–12w	-	4w
Abandoned	26–27d	-	-	-	-	-	4w

w = weeks, d = days

Discussion: A single developmental pattern is evident. The young ride continuously during the first week (less if the water is very warm), and intermittently until two or two and a half weeks. They first dive for food during the second or third weeks, but do not feed themselves until nearly four weeks. If the adults stay with them longer, they continue to beg until six or more weeks.

Description of behaviour: The young of all species climb onto the parent's back as soon as they are dry after hatching. They are fed, either by the other parent or by the parent carrying them, while they are in the feathers. Insects and feathers are presented from the first day, and they are dabbled in the water before being offered. The adult holds the food in the tip of the bill and lowers the bill forward from the resting posture until the food is on a level with the chick's bill. The chick then reaches

forward and snatches it directly from the parent's bill. After two weeks the young often swim directly away while holding the food and then turn it around and swallow it.

At least Pied-billed, Red-necked, Great Crested, and Least Grebes, and probably all species have a soft, single-noted, species-specific call which attracts the attention of the young. It is used when the young stray away or when the adult approaches with food, but not as a continuous following call as in the ducks.

Western, Great Crested, Pied-billed, Horned Grebes, and probably all species, occasionally dive with young, but the young often pop up to the surface. They do not regularly have the young on the back while hunting for food by diving. Young are shaken off the adult's back by a body-shake or wing-flap. The adult then generally preens and bathes, and then the young climb on again or go to the other parent. The young attempt to climb at the sides or back, but cannot get up on the sides. The adult turns its tail to them, and sometimes lowers its body in the water.

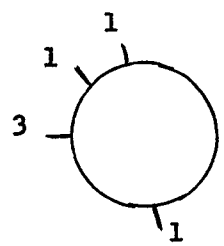
When carrying young the parent holds the wings tightly closed against the flanks but spreads the secondaries and lifts the scapulars slightly making a pocket under each wing. The young may be concealed there or ride with their heads out between the scapulars. As many as five may be carried by one bird while the other feeds them. Later the brood is sometimes divided, each parent leading and feeding only its own charges.

HATCHING

The chick breaks through the inner shell membrane and starts to cheep between 12 and 36 hours before hatching. The calls are the same as those after hatching, given irregularly in bouts of 2 to a dozen calls repeated every few minutes. The calling itself has no special features, but it stimulates the parent to steady incubation during this period.

Pipping is done by pecking with the tip of the bill armed with egg tooth material on both the upper and lower mandibles. Because of the position of the bird in the egg, the pip hole was always at the blunt end about one third of the distance from pole to pole. In six Western Grebes the position of the pip hole in the vertical dimension was determined. See Table III.

Table III. View of the Blunt End of Egg Showing Place of Pipping



After pipping the bill is extended out the hole and levered back so that the upper mandible strikes the unbroken shell and makes a path through it. The whole bird turns only slightly in the shell during this process. When the broken path through the shell has reached 90° in a counterclockwise direction from the pip hole, the whole neck of the bird comes into play. The neck is curved in a complete circle around the blunt end of the egg, and with the help of the legs it levers against the blunt end of the shell. The shell splits cleanly 90° clockwise from the pip hole, and the blunt end cap is bent back shattering the remainder of the circumference of the circle

(observations on eight hatchings). In one instance where the movements were counted there were fifty head movements irregularly spaced in 53 minutes making the first path. The neck levering required only 4 movements in two minutes to break off the cap and get the chick out.

Hatching from the first pipping took 50 minutes to two hours under incubator conditions. If temperatures are lower the activity of the bird is depressed, and one egg held in the hand required five hours to hatch. Hatching is usually a slow process in birds, and Nice (1962) suggested that the speed of hatching protected thechick against the danger of drowning in the wet nest. The nest is always completely saturated, but seldom does it have standing water at the end of incubation. The nest is continually added to during incubation, and the water level of the lake often drops one or many inches adding to the dryness of the nest. However the weight of the adult on the pipped egg might be enough to force water into the hole and drown the chick.

At hatching the yolk sac was completely enclosed, and the aperture was barely visible. Each down feather was enclosed in a thin silvery sheath. The feathers expanded first on the belly, then the breast, then the back and finally the head. The back feathers were fully expanded after three to four hours under the brooder; the head feathers took a further two hours. In the incubator with its higher temperature drying was completed quickly, but the feathers expanded at the same rate as in the brooder. The sheaths broke simply as a result of drying; the birds did not preen and are not preened by the parents. Friction against the floor or other birds was slight as the birds were relatively quiet until dry. See Table IV.

Comparison: Ducks, gulls, and many others pip the shell a day or more before hatching. The membranes are allowed to dry slowly and the chick works gradually at the hard shell. Vermeer (1963) gave the hatching

time for Glaucous-winged Gulls as 1 to 5 days, mean 3 days.

Herring Gulls (Tinbergen 1953) turned in the shell, presumably balancing the gravity sensitive organs in the ear, and pipped the shell within a few degrees of the top. Once the shell is pipped, the adult does not turn it. Young gulls in nests on beaches would become contaminated with sand if they pipped near the bottom of the egg. Grebes seem to pip the shell fairly high, but the first 90° turn brings the head right down to where the nest is wet. Presumably the speed of hatching is enough protection in most cases.

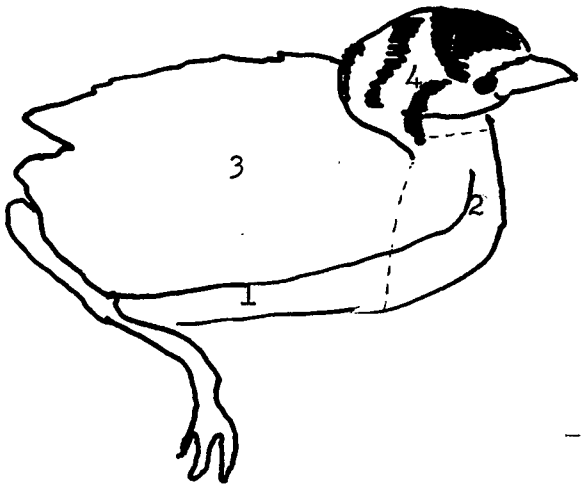
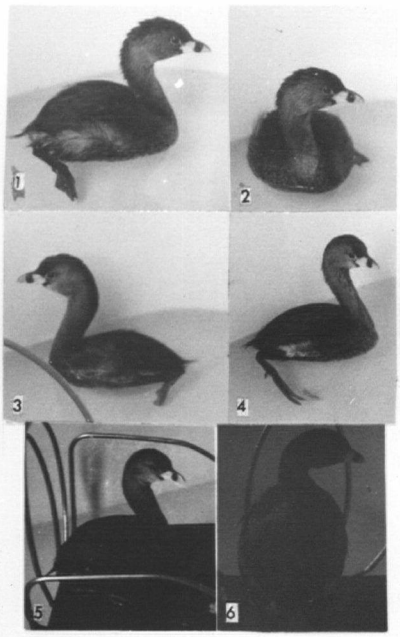


Table IV. Areas in Order of Drying after Hatching

hours	1	2	3	4	5	6
area			3		4	

Plate I. Behaviour of Adult Pied-billed Grebe.

1. Normal swimming posture, side view.
2. Normal swimming posture, front view.
3. Low-intensity alarm.
4. Medium-intensity alarm.
5. Low-intensity alarm on platform.
6. Normal standing posture, rear view.
7. Nibbling oil gland.
8. Nibbling oil gland.
9. Rubbing head on oil gland.
10. Drinking, first stage.
11. Drinking, third stage.
12. Drinking, second stage.
13. First stage of wing-flap.
14. Beginning of body-shake.
15. Beginning of body-shake.
16. Second stage of body-shake.
17. Second stage of wing-flap.
18, 19, 20, 21. Bathing, head-dipping.
22. Walking, normal posture.
23. High intensity alarm on platform.
24. Normal walking posture.
25. Walking in alarm posture.
26. Running when chased.
27. Running when not being chased.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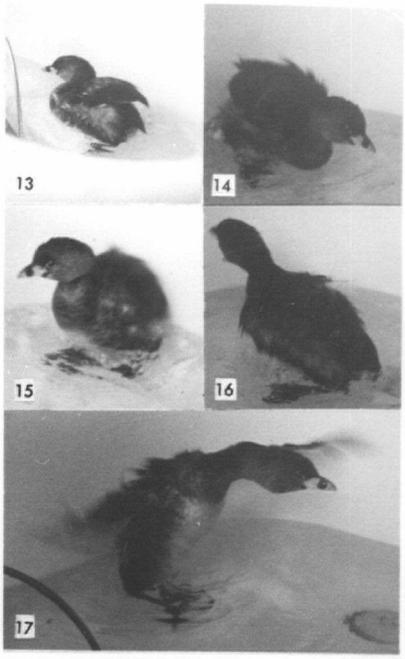
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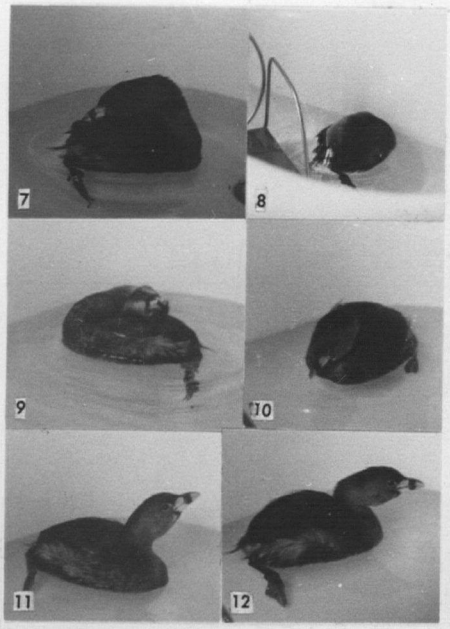
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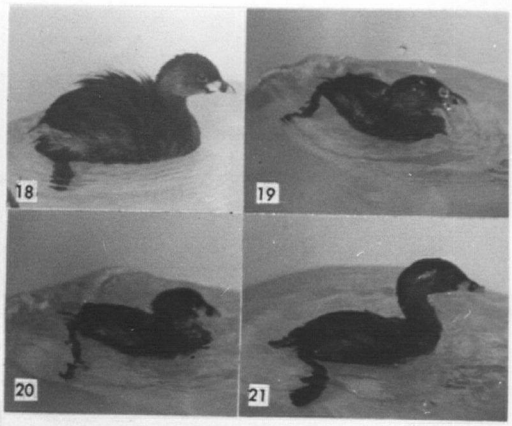
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RESTING AND SLEEP POSTURES

Problem: At hatching the birds are physically capable of assuming the sleeping posture from the resting posture, but the head and extremities drop until supported on the substrate. They are repeatedly returned to their positions, but the full sleeping posture cannot be maintained until two weeks of age. The young sleep longer and are less easily disturbed during the first two weeks than later, and the slow development of the sleeping posture is a combination of muscular development and increasing wakefulness. Until the sleeping posture is fully developed, the young bird sleeps on the parent's back. It cannot sleep on the water, and on land the eyes would be irritated by contact with the substrate.

Resting Posture

Description: There are two postures, one a relaxed resting posture, and the other that used in sleep. The two are linked by a continuous chain of intermediates. In resting on a platform the adults and older young kept their feet facing straight forward on the platform beside the body with the toes together, lobes partly closed. The neck was angled slightly back of vertical with the occiput on the scapulars and the base of the bill directly over the front of the breast and horizontal. The tail was straight out behind and the wings were often lifted slightly from the back feathers at the rear. A full side view is shown in figures 2 and 3, and a top view in figure 4. On the water the body, head, neck, and tail positions were the same, but the feet dangled in the water with the tarso-metatarsus at forty-five degrees forward and the digits almost straight down. The tail sometimes floated on the water.

Occurrence: The resting posture was the posture used by all grebes when awake and not engaged in some other activity. It was used little during the first week when the birds slept most of the time, but its use increased until it occupied many hours of each day.

Species variation: The head and body positions were the same but the necks of the longer-necked species were more curved to maintain the head with the occiput on the shoulder girdle. Photographs of the resting postures of Eared, Red-necked, and Western Grebes are shown in Plate III. Front views are shown in Plate II, numbers 2, 3, and 4, and resting of an older downy with wings on the back appears on Plate II, number 1.

Development: At hatching the adult posture was taken except that the wings were extended to the sides with the carpometacarpus flat on the substrate about sixty degrees forward from the longitudinal axis of the body. On the water the wings floated fully spread at the sides of the body, the neck was forward, and the head was just above the surface of the water. By the end of the first day the wings were repeatedly flipped up onto the back while the bird was on land, but there was still no attempt to keep the wings out of the water. On the fourth day the wings were maintained on the back in the adult manner, and the occiput was held up on the shoulder girdle.

Comparisons: The adult resting posture described above is the same as that taken by ducks, loons, alcids, gulls, and all others which rest floating on the water. All precocial birds except loons and grebes take this posture in the adult form from a few hours after hatching.

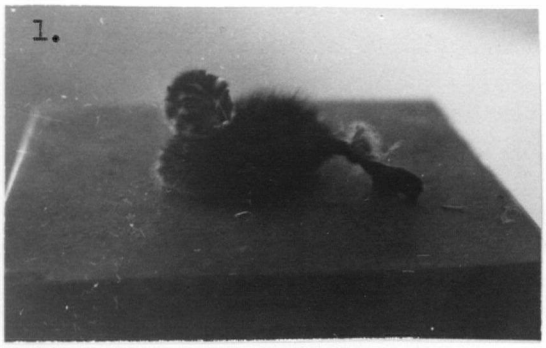


Plate II. 1. Resting posture of older Eared Grebe with wings on back. 2,4. Resting posture of newly-hatched Eared Grebe showing wing position on substrate. 3. Resting posture of Red-necked Grebe showing wing position on substrate.

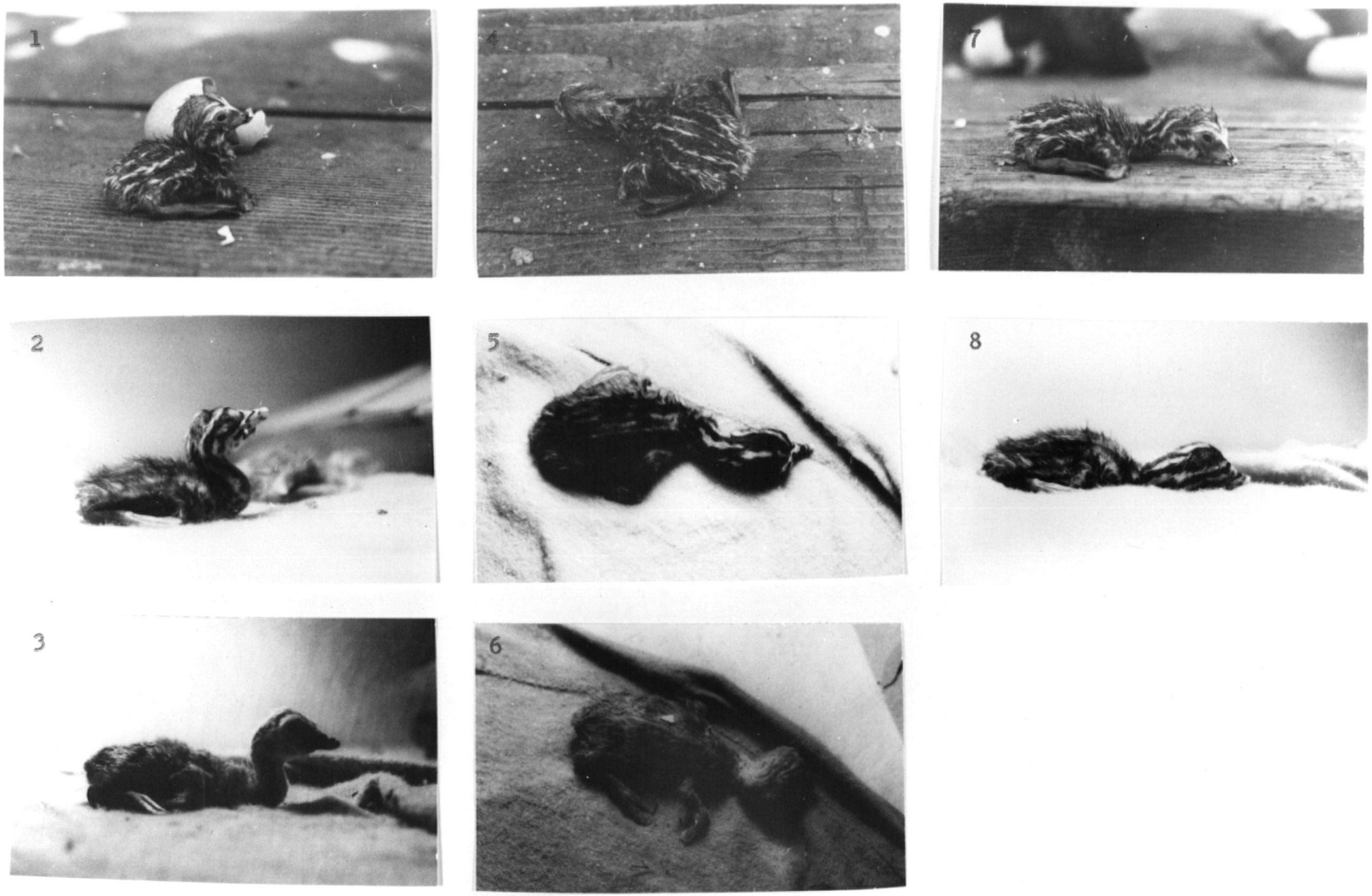


Plate III. 1,2,3. Resting postures in newly-hatched Eared, Red-necked, and Western Grebes. 4,5,6. Sleeping postures in newly-hatched Eared, Red-necked, and Western Grebes, top view. 7,8. Sleeping postures of Eared and Red-necked Grebes, side view.

Sleep Posture

Description: As the birds relaxed from the resting posture into the adult sleep posture, the wings were dropped onto the back and the head was drawn back so that the tip of the bill was over the front of the breast. The breast feathers were relaxed and fluffed out slightly, and the bill was buried in the breast feathers beside the neck (figure 5). The head in this position was slightly forward of the middle of the bulk of the body, and the bill was slightly lower than the horizontal. Then the legs and feet were drawn up, one at a time, onto the flank feathers. Figure 1 shows, from a dorsolateral view, the feet on the sides. The legs were laid on the sides just ventral to the lower edge of the closed wings, and the flank feathers fluffed up over them making them completely invisible in the adult. In the young the down of the sides and wings was not long enough to cover the feet. The usual curve of these flank feathers over the lower edge of the wings can be seen in Plate I, numbers 1, 2, and 10. The feet were not drawn up when captive grebes were on the water, probably because of lack of space for drifting. Finally the eyes were closed for brief periods.

Occurrence: The first few days the young birds slept all the time except when feeding. They slept motionless for fifteen minutes or more when alone, but when touching another bird they changed position much more frequently. Sometimes the eyes were simply opened and then closed. Often the head was lifted with or without opening the eyes. Each time the bird woke, it started again with the resting posture and closed its eyes and relaxed into the sleeping posture. What comfort movements were seen were done while the birds were stirring in their sleep or when wakened momentarily by the movements of other birds. By the end of the first week about

half the time was spent in actual sleep. Intervals were spent in preening, bouncing around, or begging for food. At first the young grebes would have been kept constantly on the parent's back and having them still would be an advantage to the parent. By a week they would be spending some time on the water. When they moved around wakefully on the parent's back they would either fall off into the water or be shaken off by the adult.

All the young slept all night when in the dark. Under a lamp they maintained their daytime routine of sleep and begging throughout the night.

Adults in captivity slept about one third of the time during the day.

Species variation: Pied-billed and Eared Grebe adults buried their bills in the median ventral breast feathers. Red-necked and Western Grebes (and the Great Crested Grebe) put the beak to one side of the neck. The longer neck of these last species was doubled far back on the back of the bird in the posture referred to in Simmons (1955) as the "pork-pie posture". Heinroth (1928) stated that in the Great Crested Grebe the bill was actually clamped under the neck. In view of the several lateral movements used to put the bill into the breast feathers after the neck is down on the back, this is probably not so. The beak was never seen turned to the back as Aldrich (1929) reported for a Horned Grebe and Shelley (1930) reported for a Red-necked Grebe.

In the first sleep posture of the young the head dropped forward from the resting posture until the bill touched the ground. This meant that regardless of the length of the neck the bill was the same distance from the body in all species. The neck remained in a similar s curve as was seen in the resting posture. Photographs of the sleep postures of newly hatched Eared, Red-necked, and Western Grebes are shown in Plate III.

Western Grebes did not show foot-lifting. They simply curled the toes under while the legs were held at the sides. They kept the first sleep posture through the eight days they were observed.

Disturbance during sleep: Loud noises or vibrations caused no disturbance of sleep. Sweeping within a foot of the birds, hoses, metal boxes dropped on the concrete floor on which they slept did not wake sleeping birds or disturb those awake. One bird waking and calling for food did not disturb the others unless it touched them. This singular lack of response to moving or noisy objects nearby is in marked contrast to the behaviour of other precocial young which are startled by voices or objects moving even at a considerable distance.

Development:

First sleep posture: In the first three days from the resting posture the eyes closed and bill dropped until the tip touched the ground about one inch in front of the base of the neck. Then the head drooped over to one side or the other until the side of the head rested on the floor. Left and right head positions were seen about equally. Occasionally the bill slid forward on the floor until the ventral surface of the neck and bill were on the ground. In either final position the neck was contracted, and the head and neck together about equalled the length of the body. At the same time the wings if on the back slid off until the carpometacarpus was flat on the ground. Then the carpometacarpus tended to slide forward and away from the body until it was about sixty degrees forward of the body axis. On a soft cloth substrate the wings may not slide away from the body, and remain touching the floor parallel to the body axis. The legs were flat on the floor with the tarsus having the sharp dorsal aspect on the floor. The

lobes of the phalanges were flat on the floor, not folded, and overlapping so that the digits themselves were close together. The feet slowly extended to the sides, the foot in a straight line with the tarsus, until the flat mesial aspect of the tarsus faced the floor and the lobes of the toes were folded. The legs usually stayed straight out to the sides, but occasionally extended straight out behind. On a soft surface preventing sliding the feet remained forward and the toes might be curled down with the lobes folded and held this way for a minute or two.

From the first sleep posture the adult sleep posture was gradually assumed. The birds always started with the adult resting posture, and made active though unsuccessful attempts to maintain this posture during sleep. The first sleep posture is shown in Plate III.

Development of adult wing position: The wing was the first of the extremities to be held in the adult position. They were flipped up and dropped slowly down again from the first day. Flipping the wings up onto the back was one of the most common movements of the first three days. One wing might be so lifted repeatedly, or the wings alternated. They were seldom both lifted together. One bird might use this movement twenty or more times in an hour. The wings were maintained on the back during sleep from four days.

Development of head position: The adult sleeping posture required that the head be on the back and the bill in the breast feathers. From hatching the young bird preferred to have its head up when sleeping. It started in the resting posture with the head up, and as it went to sleep the head dropped, was raised to rest position with the eyes closed or open, and dropped again. This was often repeated a dozen times or more before the bird remained still. Many birds actively sought support for

their heads by either laying their chins against another bird or propping their bills at the side of the box. The bird then went to sleep without numerous false starts. The small spaces available under the wings of the adult would allow the heads of the young to be propped up as they slept normally on the parent's back.

Several individual birds developed unusual ways of keeping the head up during sleep. One Eared Grebe at 24 hours curled its head around until the bill was tucked under the base of the tarsus and held this position a few minutes. It did this repeatedly for an hour, and then never did it again. At five days one Pied-billed Grebe and at six days one Red-necked Grebe turned the beak some sixty degrees to the side and put the tip of the bill down with the chin on the outstretched wing. This also was not repeated.

At seven days control of the head position was beginning to be established. The birds went to sleep with the head in the adult posture, and it slowly dropped until the tip of the bill touched the floor. Then it was pulled back with a quick jerk, the bird apparently not waking. The bill was held either straight to the front or up to 45 degrees to the side, but it was not tucked into the feathers. By ten days the bill was tucked into the breast feathers, but it still dropped forward after the bird was asleep. It was not until the end of the second week that the head was held up during deep sleep.

Maintaining foot position: While asleep the bird repeatedly lifted one or both legs alternately only to have them drop down to the floor again. When the leg was on the floor forward almost parallel

with the axis of the body, the foot was lifted and flicked twice (rarely three times) downwards and outward brushing the side feathers and ending with the leg perpendicular to the body axis. The foot was kept in a straight line with the tarsus, and the digits didn't bend. Then the leg was lifted onto the back above the wing as it lay outstretched and laid on the back with the toes touching the base of the humerus. There was no depression in the down at this place and the down did not extend over the leg or foot.

Putting the foot up on the back during resting is the most common of all movements in the first two days, and was seen from two hours after hatching. By six days one Pied-billed Grebe slept regularly with the feet in the adult position on the back. The down was fluffed over the legs but was too short to conceal them. By this time the wings were held on the back during sleep and the leg lay along the lower border of the folded primary feathers. As the wings developed, they extended further and further down the length of the tarsus. The lengthened down fluffed over the leg and touched the wing, thus concealing the leg progressively more and more. It was not until after the fourth week that the heel joint was completely hidden. The timetable of development of the sleep posture is shown in Table V.

Table V. Development of Adult Sleeping Posture, Pied-billed Grebe.

	Appears	Maintained
Wing on back	first day	4 days
Feet in flank feathers	first day	6 days
Head on shoulders	first day	14 days
Bill in breast feathers	10 days	14 days

Comparison: Sleeping with the feet up and the bill in the breast feathers seems to be confined to the grebes and loons. Gruiforms, charadriiforms, and Anatidae often sleep standing on one foot with the other in the flank feathers, or swim with one foot shipped away, but they seldom have both feet up. Many groups rest with the head forward, but all turn the head back into the scapulars to sleep, except the loons and grebes.

All precocial birds sleep with their heads up from a few hours after hatching. When the galliforms, charadriiforms, and anatids first turn their heads back under the scapulars has not been noted. It is a number of days before ducklings sleep standing on one foot, and young galliforms sleep on a perch. The semiprecocial gulls do not hold their heads up in sleep for several days, and did not place their heads in the scapulars until five and seven days (Franklin's Gull, Nice 1962).

In passerines (Nice 1943) instead of a gradual assumption of the adult sleeping posture, there is a sudden change from the nestling posture to the adult posture. The change is closely correlated with leaving the nest. In Song Sparrows the adult sleeping posture first appeared the day the birds left the nest or the day after. In the hole-nesting House Sparrow where the time in the nest is greatly extended, the resting posture appeared at the same stage as in the Song Sparrows, about 10 days, but this was six days before they left the nest.

Young grebes slept much more than precocial birds of the same age. When ducklings were kept with the grebes, they wandered around and fed while the grebes slept. Since precocial birds must follow the adult, and many must feed on small material which they gather themselves, it is necessary that they be wakeful and active. Grebes do not need to follow

the adult or feed themselves, and there is a distinct advantage to their being still on the parent's back.

Because of their inability to hold their heads and eyes off the substrate during the first week, grebes must sleep in a clean place preferably with the head artificially supported. When the downy grebes were allowed to sleep on a particulate substrate, their sleeping posture allowed the eyes to come in contact with the litter. Their eyes became filled with bits of the litter, watery and mucus filled, and they became blind and unable to eat. Occasionally ducklings in the hatchery at Delta also developed swollen eyes from contact with peat moss litter (Peter Ward, pers. com.), but this was normally not the case. Young grebes could not be raised in nests of sand or gravel such as those used by charadriiforms, and only with difficulty in the stick, reed, or forest litter nests of Anatidae, Rallidae, and galliforms. The eyes of altricial and some semialtricial birds are closed until the fourth or fifth days, protecting the eyes from contact with the nest until the bird is strong enough to control the movements of the head more adequately. Also most altricial birds are confined in a nest small enough and cupped enough to support the young in a compact position, keeping the eyes from contact with the nest material.

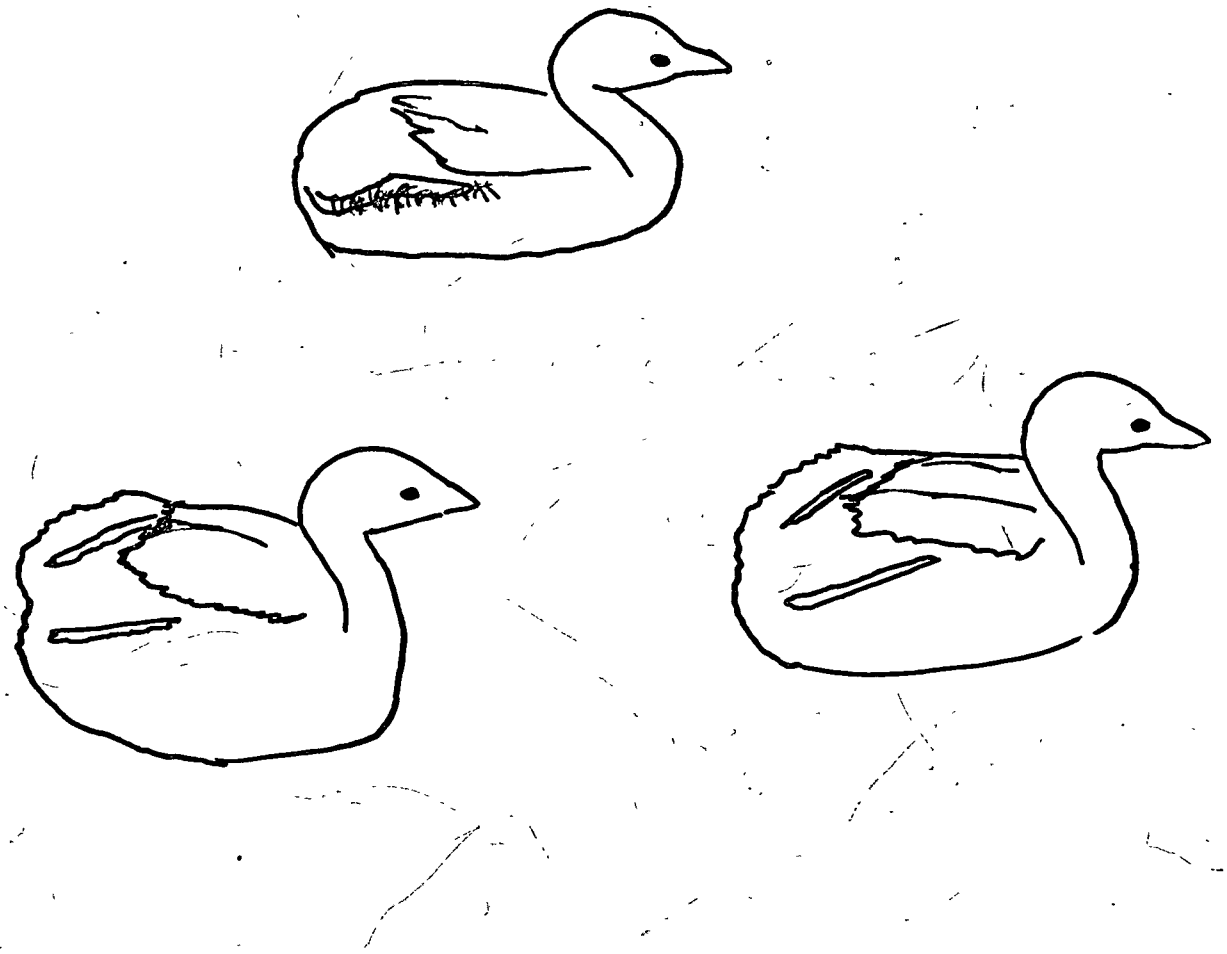


Fig. 1. Resting with the feet up on the back, slightly dorsal view. Pied-billed Grebe, three weeks old.

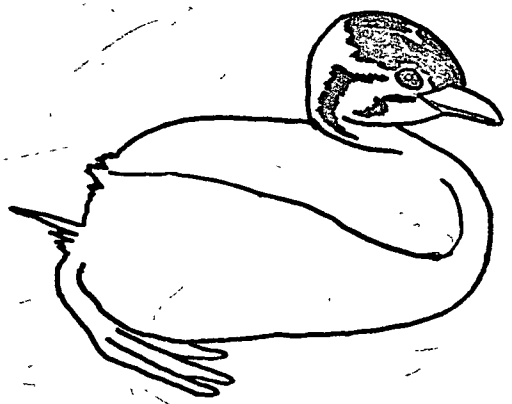


Fig. 2. Resting position with feet on substrate.

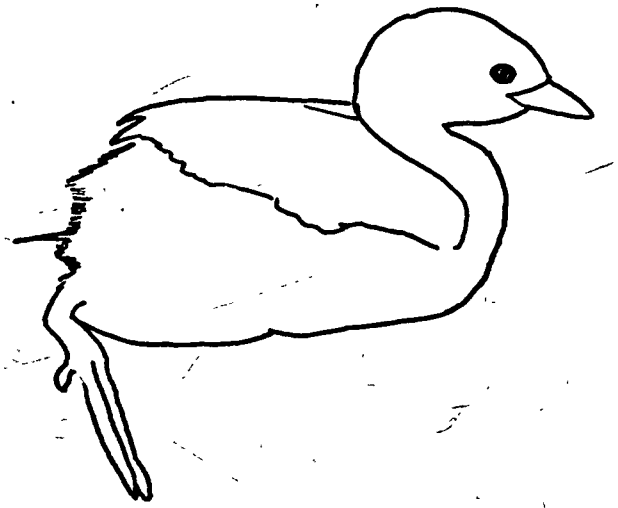


Fig. 3. Resting on platform with feet dangling.

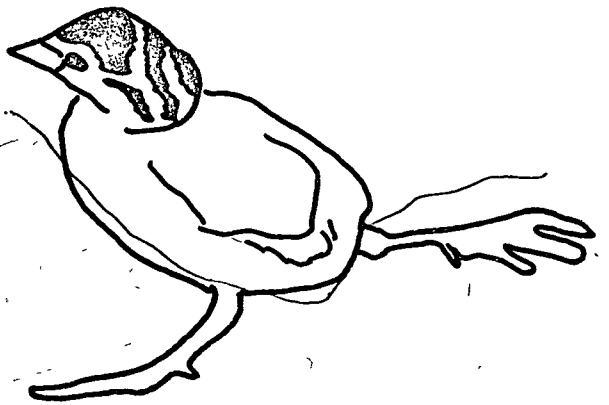


Fig. 4. Resting in water, wings held on back.

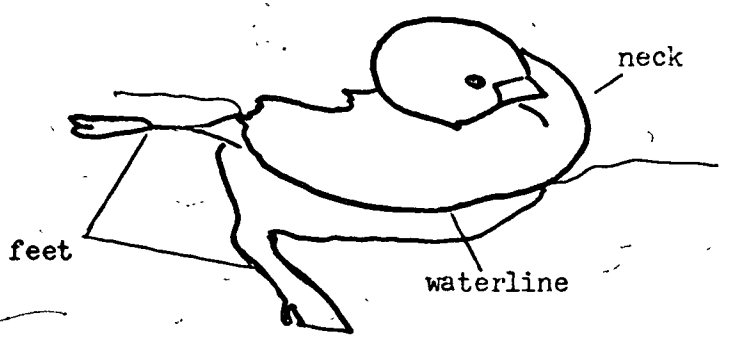


Fig. 5. Sleeping posture on the water with bill tucked in breast feathers beside neck.

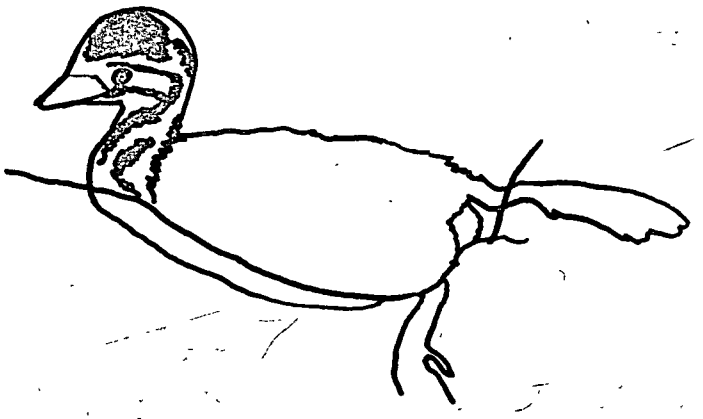


Fig. 6. Normal resting posture on the water. Slightly dorsal view.

DISTURBANCE CALL

Only one call was used during the juvenal period. This was a species specific multi-functional disturbance call.

Description: The normal swimming posture was used during the call, the head was horizontal and the neck extended. The bill was not opened, and the hyoid was not conspicuously depressed. The call was also given when the bird was begging and the mouth open, but there was no change in pitch. At the lowest intensity the call was repeated regularly every two or three seconds. As the intensity increased the frequency increased to once every second and the call grew louder and more insistent, but the pitch did not change.

Occurrence: The disturbance call was associated with hunger and chilling. When two hours had elapsed since the last feeding, calling occurred before the begging posture was assumed. The bird moved around and called at a low intensity, and then when it saw the observer, it assumed the begging posture and called at a higher intensity. The intensity depended on the time since the last feeding. Calling stopped when the bird was fed.

When the motivation was chilling, the call was associated with overtaking and climbing-up movements. The intensity of the call depended on the degree of chilling and the vigour of the associated movements. Calling was also seen when the bird had been following or overtaking and the leader got outside the preferred distance. The bird then stopped overtaking or following and stayed in one place calling. The function of the call in all instances is to attract the attention of the parent to the chick. The parent responds by either offering food or allowing the chick to climb up on its back.

Species variation: The calls of the Pied-billed, Horned and Red-necked Grebes were chicken-like in quality and nearly identical. The Western and Eared Grebes had lower, more gutteral calls, that of the Eared lower than that of the Western Grebe. The functions and associations of the calls of all species were the same.

Development: The juvenal call did not change in the period in which these birds were held in captivity, Western one week, Red-necked two weeks, Eared three weeks, and Pied-billed seven weeks. In the oldest Pied-billed Grebe there was a very slight lowering of pitch, but the character and use of the call remained unchanged. This call probably develops into the similar species specific single-noted call of the adult. The adult disturbance call is the only adult call heard all year, and it is a multi-functional call seen in captivity when the bird is hungry or restless.

Comparison: The young of galliforms, ducks and others also have a single-noted call used when the chick is hungry, cold, or lost.

LOCOMOTION

Swimming

Description: In ordinary swimming of adults the head, neck, body, and tail were as in resting, and only the legs and feet moved. In simply holding position in the water, the tarso-metatarsus was not moved and the digits moved forward to a straight line with the metatarsus, spread, and moved back to vertical. The feet were always used alternately, although one might be held stationary while the other sculled a few short strokes affecting a turn. In slow swimming the tarso-metatarsus was moved slightly downward on the down stroke of the digits. In faster swimming the tarso-metatarsus was brought down to a vertical position on the downward stroke. When the bird was not alarmed, the head and neck were held in the same position regardless of swimming speed. The normal swimming position is seen in Plate I, numbers 1 and 2.

Occurrence: Adults are on the water except when incubating; most of the time they are swimming. The young swim only enough to reach the parent and climb on its back. Time on the water gradually increases from the sixth or seventh day until the adult situation is reached at two and a half weeks.

Species variation: No species variation was noted except in the position of the head and neck. In the adults the longer the neck, the higher the head was held and the more curved the neck was. The necks of Eared and Horned Grebes were nearly straight, the Pied-billed more curved, and the Western Grebe the most curved. In the first swimming posture of the young the same differences were seen. The lower part of the neck was in the water in the Eared and Pied-billed Grebes and the dorsal surface was above.

In the longer necked Red-necked Grebe part of the neck and in the Western Grebe the whole neck was in the water as it was arched to keep the head close to the body. Simmons (1955) described the young of the long-necked Great Crested Grebe swimming with the neck awash.

Development: Young grebes can swim from an hour after hatching, but slowly and only for a few minutes. They do not use the swimming posture of the adults, however. The wings and legs were spread straight out to the sides on the surface, and the head was held back close to the body with the neck more or less in the water depending on the species. The legs were used alternately and very rapidly, moving almost directly in a horizontal plane.

At four days the wings were still extended on the water, but by five or six days the wings were held closed on the back. The wings in resting on land were first held on the back on the fourth day. The body itself was at this time more erect and in the Pied-billed, Eared, and Red-necked Grebes the head was held on the shoulders as in resting. The Western Grebe carried its head somewhat forward with the ventral surface of the neck in the water until ten days (no later observations). See figures 4 and 6.

Comparison: The position of the body and head is similar to that used by all waterbirds, but the use of the legs is unique to loons and grebes. The legs are placed as far to the rear as is possible, and they are directed to the sides so that the direction of the thrust is to the side on the same level as the body instead of below it. As in other groups with lobed toes, the toes are bent and the lobes fold on the recovery.

Fig. 7. Swimming with tail up. Right front view.

Alarm Posture

Description: As the bird became alert, and then alarmed, the neck was extended so that the distance from the angle of the chin to the water increased from 40-50% of the body length at the waterline to 60% or more of the body length. The feathers on the neck were flattened as the neck was stretched. The feathers on the mid-dorsal line of the neck were sometimes slightly raised, but this did not correspond to the degree of alarm. The backward angle of the neck was sometimes slightly increased, but the head position remained horizontal. Although the extension of the neck would seem to increase the view of the surroundings, there were no lateral head movements. The head was usually motionless, or at most slowly turned towards the source of alarm. The wing and back feathers were compressed, and the body was lowered slightly in the water. Leg and foot positions remained the same as those used in swimming. The alarm posture of an adult Pied-billed Grebe is shown in Plate I, numbers 3, 4, 5, 23 and 25. Alarm in a young Pied-billed Grebe is shown in figures 8 and 9.

Occurrence: Alarm is not often seen in wild birds during the winter and spring, but it becomes the habitual posture of nesting birds. It was seldom seen in captives, and never at a very high intensity except when they were chased.

Species variation: No variation was seen in the basic posture. In one instance an adult male Pied-billed Grebe was seen to raise the tail and spread the white under-tail coverts in the alarm attitude. This was not a regular part of the alarm posture of captive Pied-billed Grebes, and its significance is not known. Raising the tail, if present in the other species, is not conspicuous.

Development: The alarm attitude was in the functional form when it first appeared. The body and neck feathers were compressed as in the adult, but the down cannot be pulled as close to the body as contour feathers, and in this attitude the young bird was not as slim as an adult.

None of the captive chicks used the alarm posture in the first two weeks. At 17 days a low intensity alarm reaction to a loud noise was seen in one Eared Grebe. This was the only use of the alarm posture in the three and a half weeks this bird lived. After three weeks the posture was more common in the Pied-billed Grebe which was successfully raised. Its appearance is correlated with the increase in the use of diving as a means of escape.

Comparison: The alarm posture is an intention movement of and preparation for diving. A similar movement is present in loons, diving ducks, and cormorants, but in ducks and others whose primary means of escape is flying, the alarm posture is a preparation for flight.

The compression of the feathers in grebes increases the specific gravity of the bird by reducing the volume. One six ounce Little Grebe with a volume of 13 cubic inches lost 2.24 cubic inches when the feathers were bound down as in the alarm posture (Stubbs in Schorger 1947). Compression reduces buoyancy by pressing out the air usually trapped in the feathers. The specific gravity of diving birds is higher than that of birds which do not dive, because of a decrease in pneumaticity of the skeleton paralleling increase in diving ability. Pneumaticity of the bones is slight in grebes, diving ducks, and cormorants, and absent in loons (Streseman in Schorger 1947). The absolute specific gravity of

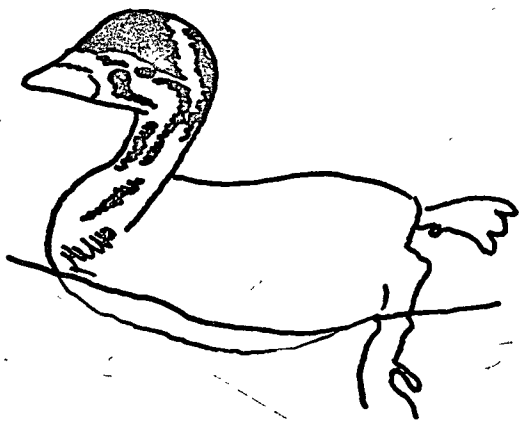


Fig. 8. Medium intensity alarm posture on water.

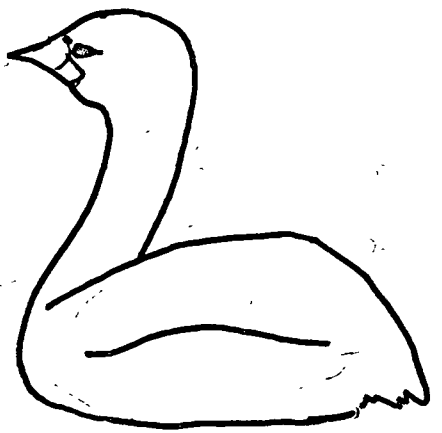


Fig. 9. Medium intensity alarm, adult Pied-billed Grebe.

one freshly killed Little Grebe was 0.86, when the bird was dry and clean with plumage as large as possible 0.66, and when the feathers were bound down in as natural a position as possible 0.84. The remaining difference between specific gravity of the bird and that of water is eliminated or almost so by compression of the air sacs.

Young grebes whose down was soaked replaced the usual air envelope with water and actually sank. Ducks (Schorger 1947) freshly killed floated.

Diving

Description: In the normal feeding dive the head was not brought back from the resting position. It was put forward and down in a single motion with the occipital joint still bent as it was on the back. This left the neck straight forward and the bill straight down. The movement took less than one sixteenth of a second. The forward motion lifted the wings and scapulars slightly at the posterior end but did not affect the tail. The first foot thrust pushed the body half under water, and a second thrust completed the dive. Both feet were used together and almost directly out to the sides in the kicks. As the water contacted the scapulars and body feathers, they were laid flat. By the middle of the first foot thrust the bill had been brought to a forward position and the neck was almost straight. Each thrust lasted about a quarter of a second, the whole submergence lasting half a second or less (Table VI). The sequence up to the end of the first thrust is shown in figure 10.

When the birds dove from the alarm posture, the feathers were already laid down but otherwise the same sequence was followed. The birds never raised their wings in a panic dive such as that described by Lawrence (1950). They also never sank out of sight. In this pattern (Heinroth 1928) the bird assumes the alarm posture with the feathers compressed to the maximum and then kicks vigorously and simultaneously upward so that the body sinks into the water. When body and neck are under water, the head is put forward as in the feeding dive. This must require controlled manipulation of the air sacs to increase the specific gravity to as close to that of water as possible.

Table VI. Timing of Feeding Dives, Young Pied-billed Grebe

Arching head down	Kicking body under
3	8
1	5
1	4
1	4
2	4
1	4

time in 16ths of a second.

Occurrence: Young grebes can dive feebly from a few hours after hatching, but they do so only when chased. They are not frightened by any noises or by objects or animals approaching slowly. Their escape from objects overtaking them rapidly is to climb up on the parent's back. Failing this they attempt to dive, but diving as a functional escape method is not present until spontaneous diving appears after the tenth day. One incomplete dive was seen in a Pied-billed Grebe at seven days, but usually no diving was seen until ten days, although the birds were allowed to swim every two hours from hatching. Diving gradually increased until at two and

a half weeks wild Pied-billed Grebes spent most of their time diving, and captives dove repeatedly when allowed to swim.

Species variation: None.

Development: The wings trailed slightly to the sides in swimming until five days, and were dragged in diving during this time. When spontaneous diving appeared, it was in the adult form.

Comparison: Young loons ducked their heads under the water when less than a day old, but were unable to kick their bodies under. At just over a day they were able to make dives of two or three feet at a depth of eight or ten inches, at two or three days five to ten feet at a depth of three or four feet, and at six or seven days forty to sixty foot dives at depths greater than ten feet (Olson and Marshall 1952). These records are presumably from birds which were chased.

Coots first dived at 6 days, at the beginning of stage V (Gullion in Nice 1962).

Adaptive correlates: The scapular contour feathers grew to precisely cover the wings by eighteen days and thereafter kept pace with the growth of the wings. Their function is to improve the rounded contour of the body and to cover the easily wetted down of the wings. The wings are adequately covered by the scapulars by the time that the birds begin to dive frequently. Also the intricate relationship of wings and scapulars might well be an argument against the former use of the wings in swimming under water, either as young or as adults.

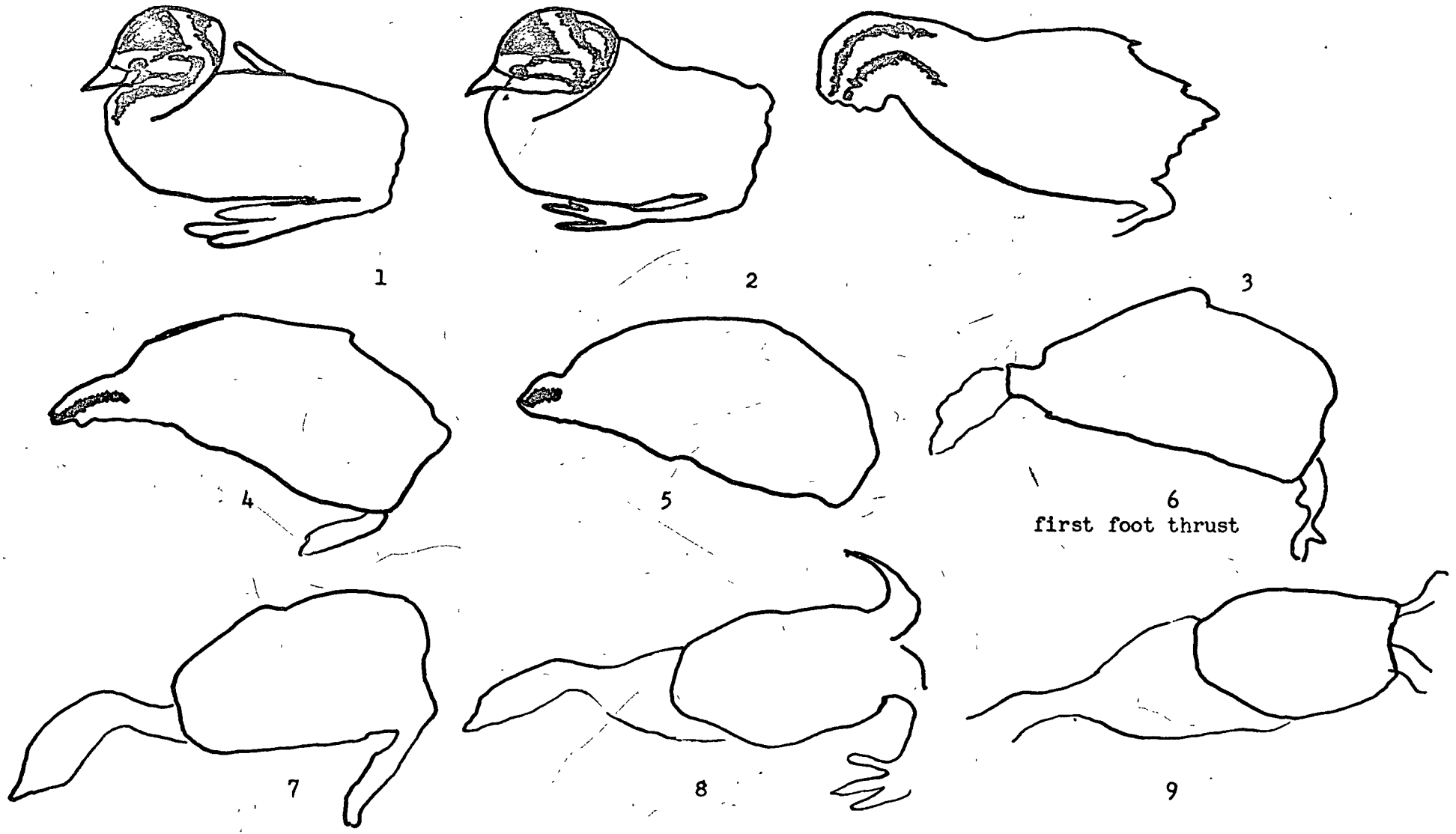


Fig. 10. Diving.

Peering under water

Description: While swimming on the surface the head was put forward as in the first movement of a dive, but more slowly, until the neck was forward and the bill straight down. The head might be submerged just to the eyes, but often the whole head and neck were under water.

Occurrence: Not often seen.

Species variation: None.

Development: Peering under water was used in the adult form from the third day in some individuals.

Comparison: In loons (Olson and Marshall 1952) it was commonly observed when the birds were not feeding but merely cruising about. Young loons, as in grebes, used this pattern from the first day. It is much more common in loons than in grebes.

Swimming under water

Description: The feathers were compressed and often covered with air bubbles pressed out of the plumage during the dive. The head was straight out and the neck slightly bent. The feet were used simultaneously, the thrusts out to the sides and almost horizontal. They began well in front of the middle of the body and continued until the feet were straight out behind. The grebes seldom swam straight ahead, but in elaborate zig-zags, and the head was in constant motion peering around. Their ability to navigate at this speed was amazing. Even in a small tub with the legs of the platform to avoid, they never touched an obstacle.

Allen (1961) showed in photographs that the thrust of the feet was

angled either above or below the plane of the body as needed for changes of direction. At the beginning of the thrust the feet could be considerably above or below the head.

Species variation: None.

Development: This pattern was in the adult form from the beginning. Only a few strokes were taken under water after the first dives, but the length of the dives and the complexity of the movements under water gradually increased.

Comparison: In the nineteen twenties there was considerable discussion whether or not loons and grebes used their wings under water. Since then considerable evidence has been amassed all revealing that they normally, and even usually when severely frightened, hold the wings closed under water. The carpal joint may be lifted from the flank feathers to stabilize a turn, but only when wounded or very closely pursued are the flight feathers spread. See Heinroth (1928), Hanzak (1952), Simmons (1955), Lawrence (1950), and Townsend (1924). Alcids and penguins use only the wings under water, the feet being held as a rudder.

Townsend (1924) felt that progression using both wings and feet was the primitive method and that this was the pattern used by young birds and returned to by wounded adults. Olson and Marshall (1952) stated that in loon chicks both wings and feet were used in diving at least until three weeks. They said the wings were used weakly and were of little value except for stabilization. In grebes the wings were dragged in diving only during the first four days, and after that they were on the back in the adult position during all dives and while swimming under water. The wings did not aid in the stroke and their presence away from the body was simply a result of lack of development of the wings.

The feet in loons (Olson and Marshall 1952) were used in a sideways sculling motion rather than in the paddling action that is characteristic of ducks. In cormorants (Van Tets 1959) alternate feet were used on the surface, and simultaneous kicks under water. The wings were somewhat away from the body and used for steering but not for propulsion.

Standing and Walking

Description: In standing the adult birds took a position with the tarsi at about a forty-five degree angle from each other, with toes spread, the breast forty-five degrees up from the substrate and breast and body feathers compact. The head was slightly further back than in the normal resting posture, and the occiput was usually close to if not on the scapulars. The tail was often not straight posterior but tipped up slightly. See Plate I, number 9.

In sitting down from the standing posture, the head was brought forward to a point where the posterior border of the eye was over the front of the breast, then drawn back at the same time that the breast was dropped to the substrate, at which time the head was at the normal position. As the breast was dropped, the wings and back feathers were raised at the posterior, without the wings being unfolded, until at the instant of contact they were higher than the top of the head. Then the wings were lowered more slowly than they had gone up. See Plate I, number 10 and Figure 12.

The adults both walked and ran with comparative ease. In both, the tarso-metatarsus was some twenty degrees up from the floor. Plate I, number 24 shows a Pied-billed Grebe walking. The feet were held wide enough apart so that the spread lobes of the toes of one foot did not

interfere with those of the other. The angle of the body was about forty-five degrees forward, the same as during standing and running. The neck could be any length from the normal swimming posture to that of high intensity alarm. Plate I, numbers 22 and 24 show normal positions, number 25 alarm. In normal positions of the neck, the head was poised directly over the front of the breast, and the neck angled about twenty degrees back from the vertical. When the neck was extended, its angle increased to about forty-five degrees back from the vertical, and the head was over the middle of the body.

In running the neck was shortened almost to the resting position on the shoulders, and the head was just in front of the body. This shows in Plate I, numbers 26 and 27. When the bird was being chased the head was slightly further forward, and the posterior edges of the wings were lifted free from the body as in number 26. Occasionally freeing the wings led to flapping them in an attempt to take off.

They either walked or ran forward up to twenty steps before overbalancing and flopping forward on the breast with the head somewhat extended forward and the feet further back than in the normal resting posture. The head was brought back and the feet moved forward alternately and then the bird stood and walked forward again.

Occurrence: Standing and walking are rare in wild grebes. They are used on the nest, and occasionally in leading young from one body of water to another. Nero, Lahrman and Bard (1958) described an unusual nesting spot where Western Grebes walked across a sandy area to dry land nests and then walked the young to water. This is probably unique, a

result of change in water levels. Grebes ordinarily preen in the water, but they occasionally stand on the edge of a muskrat house or other solid place and preen standing. In captivity in a restricted water area, they did most of their preening on the platform provided. Hand-reared birds came out of lakes and ponds and preened standing on the edge of the shore, but this may have been a learned response.

Species variation: The smaller species walked more easily and further before flopping down than the larger ones. In the larger species the head and neck movements from side to side which balanced the steps were more exaggerated.

Development: Young birds first stood to defecate or to preen the belly on the second or third day, balancing on the rear part of the body and the spread tarsi. They often took several steps as early as the third day. At first the feet were almost out to the sides, but by the fifth or sixth day the birds attempted to keep the feet facing forward. By the end of the first week the birds walked with considerable skill, but they did not begin to stand up off the tarsus with the weight entirely on the feet until the end of the second week. By the twenty-sixth day they stood up off the tarsi frequently while preening but only for a few seconds. After this the adult walking posture replaced walking on the tarsi. Western Grebes did not stand or walk during the ten days in which they were observed.

Comparison: Loons are unable to stand up off the tarsi as the heel joint is not flexible enough. They must shuffle along on the tarsi or use the flopping-forward pattern which in grebes occurs normally only in the young.

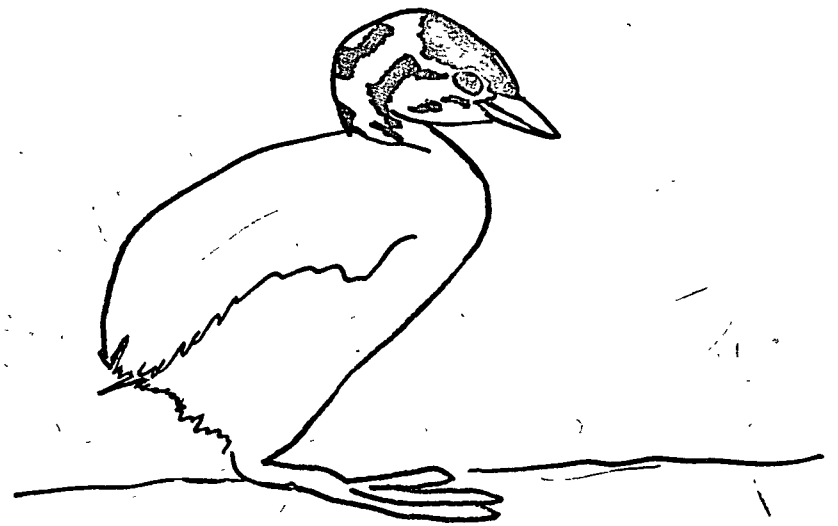


Fig. 11. Normal standing posture, direct side view.

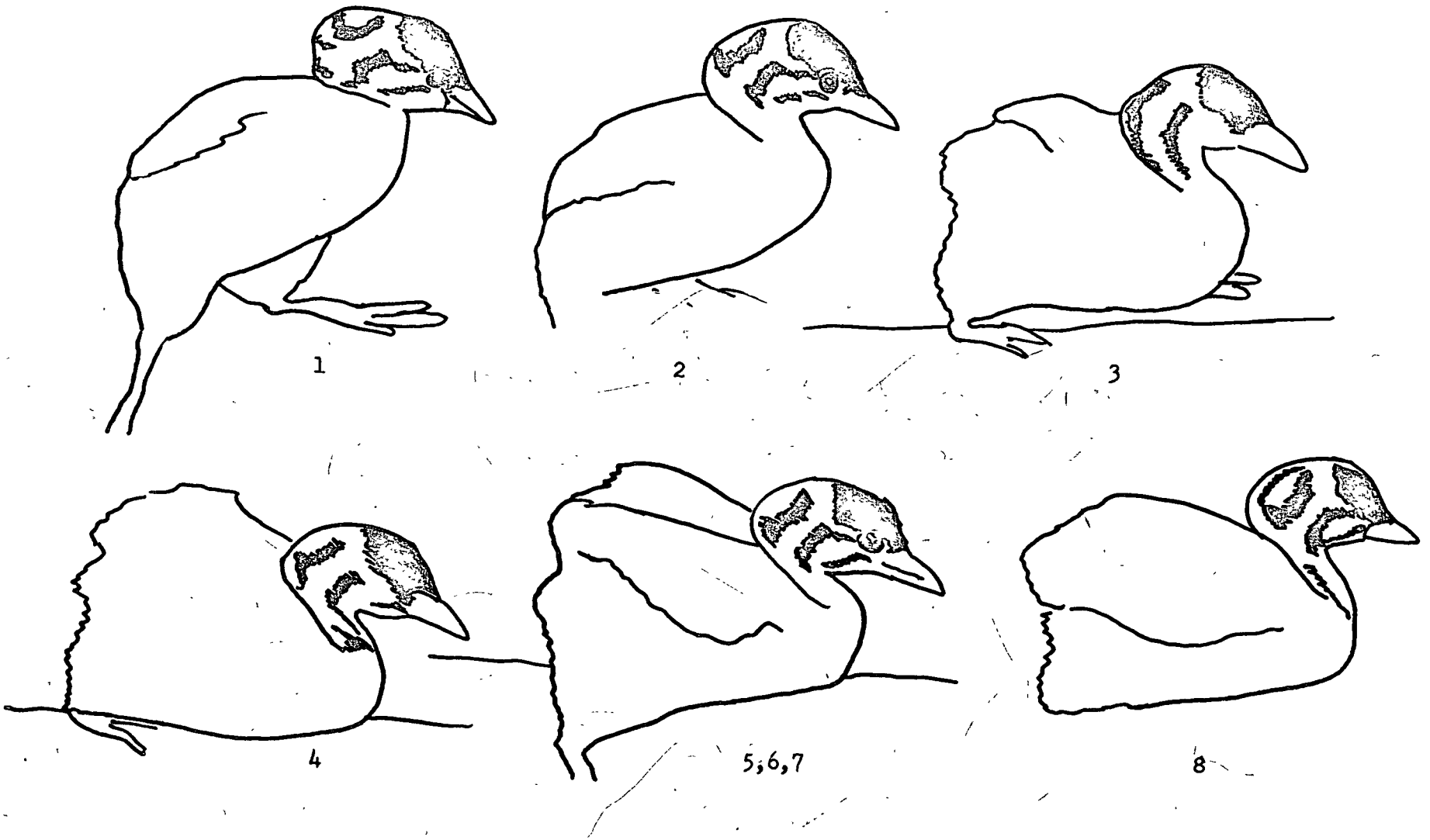


Fig. 12. Sitting down from a standing position.

Flopping-forward

Problem: Grebe chicks at hatching are relatively poorly developed and cannot stand and walk. They must be able to move across the nest before climbing on the parent's back, and to travel around on the nest when they fall off the parent.

Description: In flopping-forward the head was held nearly motionless in the normal position. The legs started under the body facing nearly straight forward. They were simultaneously brought straight back, and the back feathers were slightly raised. As the legs reached a nearly vertical position, a final quick thrust was made in which the bird was lifted forward and the legs left slightly beyond the vertical. The tail was tipped up slightly in the final thrust. In the first few days the wings were brought forward and down during the final thrust, until the leading edge of the carpometacarpus was resting on the substrate parallel to the body. Then the wings were returned to the sides, and the legs were recovered simultaneously to their forward position (figures 13 and 14). For timing see Table IX.

Occurrence: Flopping-forward was well developed at hatching, but became increasingly more rapid and efficient during the first week. Although the bird stood on the tarsus and walked by the sixth day, flopping-forward was still the predominant means of locomotion on land and did not completely disappear until walking was well developed, after the twelfth day.

Species variation: The Pied-billed, Horned, and Eared Grebes moved forward in single movement quick hops. The longer bodied Red-necked and Western Grebes divided the motion more definitely into two parts, the

forward movement and then the final lurching thrust. The compensating head and neck movements of these bigger species were also more exaggerated.

Development: The wings were used for balance while the legs were relatively small compared to the length of the body. At first the whole distal segment was on the ground, but as the bird grew, less and less of the wing was in contact until only the tip touched the ground. Finally the wings were held up on the back (from 10 days). This was not a matter of having the strength to keep the wings on the back, as the wings had been maintained in their position on the back during sleep from the fourth day.

After the first week the legs were longer proportionally and when pushed back in the first part of the thrust, they lifted the tail and rear of the bird off the substrate. In the final thrust the breast was lifted and pushed forward as before. The head was brought back in the initial part of the thrust until the tip of the bill was over the front of the breast. At the final thrust the head was thrown forward until the occiput was over the front of the breast. The wings and back feathers were rumpled up as the whole body bunched up in the initial thrust with the wings slightly lifted at the posterior. In the final thrust the body was stretched out and the back feathers laid down, but the posterior border of the wings remained slightly raised.

Comparison: Adult loons (Olson and Marshall 1952) use flopping forward instead of walking. In the young (Beebe 1907) it is used from the first day, but the chicks became less agile as they grew older.

Adaptive correlates: Flopping-forward is Townsend's (1924) "primitive reptilian scramble", the four footed method of progression to which loons and grebes were supposed to return when pursued. These two groups are so specialized in the position of the legs that on hatching the small legs are

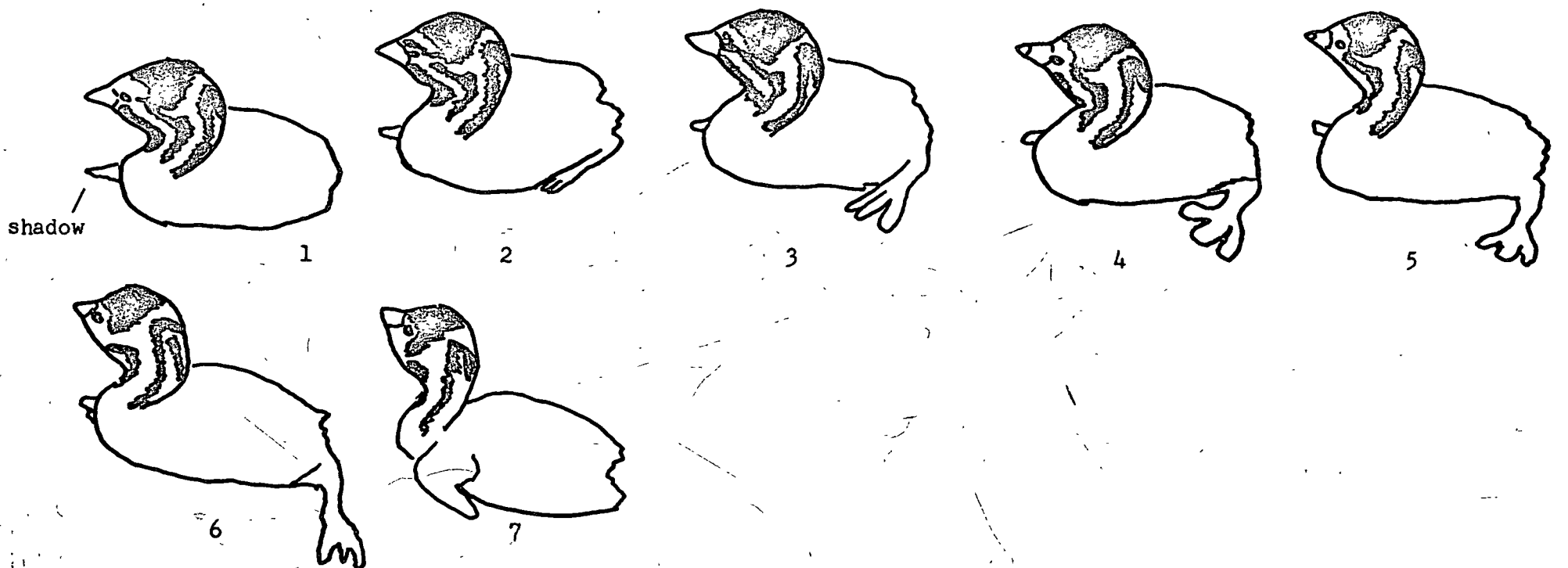


Fig. 13. Flopping forward, the first method of progression on land. Pied-billed Grebe 4 days old.

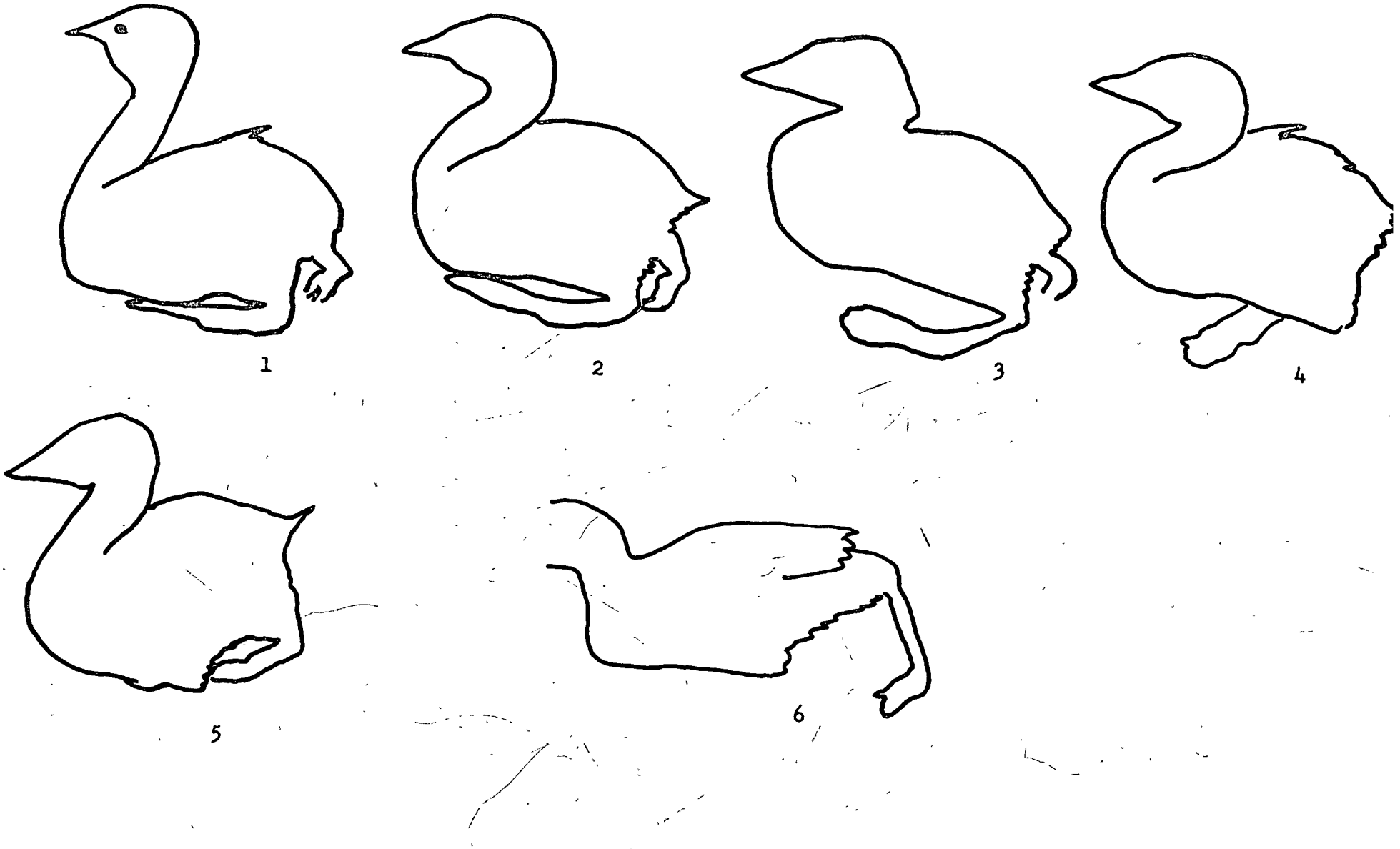


Figure 14. Flopping forward, older Pied-billed Grebe.

incapable of supporting the body. In grebes as soon as the requisite strength is attained, the adult standing and walking postures are taken. The stem group of lizards from which the birds developed certainly did not use the legs simultaneously in a frog-like manner. Nor are the wings actually used actively in these young birds; they are only extended for balance until the legs are long enough proportionally to balance the body. Flopping-forward is a secondary development necessitated by physical specialization for swimming, coupled with relatively poorly developed young, not the primitive locomotory pattern of birds.

With its simultaneous use of the feet, flopping forward is closely akin to the coordinations used in diving and swimming under water, and must have developed from them. The head position is similar to that used in resting and swimming on the surface for reasons of balance.

Climbing-up

Problem: The grebe chick at hatching is unable to stand contact with water for more than a few minutes. It cannot remain alone on the nest; its conspicuous markings would make it easy prey to crows and other predators, and the nest is cold and wet. The chick needs protection and constant brooding, and obtains these on the parent's back. In order to ride successfully it has a vigorous and highly developed climbing response, present at hatching. But the parent cannot carry the young bird after it gets too big, and it is in the interest of the birds to make this transition smoothly. The chick could be damaged if the adult attacked it when it tried to climb-up, and the feathers of the adult could be damaged in the ensuing scuffle. By

two weeks the young travel with considerable speed in the water, and the adult would have some difficulty and waste a good deal of energy keeping away from the young.

Description: The head was stretched up the object being climbed with the neck extended as far as possible. The wings were held extended as stabilizers and one or both might be flapped to regain lost balance. The feet pushed simultaneously in repeated thrusts until the downy was on top of the object being climbed. They were then either left dangling straight out behind or drawn up to the sides of the body. If the bird was well balanced, the legs were generally drawn up, but if balance was somewhat precarious they were left out behind, sometimes very stiffly. See Plate V.

A side to side movement of the head often accompanied the climbing. Its function seemed to be in finding the easiest way through the feathers to the top of the bird. The amplitude of this movement was less than an inch, the head moving more than the bill.

When an adult duck was provided for thechicks to climb, the movements were the same as those seen in the nest box. They climbed beside the tail and under the wings at the sides, but made no attempt to climb the tail. No attempt was made to grab or hold the feathers of the adult during climbing or resting on the adult's back. The chicks did not actively get under the duck's wings when on its back, but often slid under them when crawling forward. The adult grebe lifts the median portion of the wings and spreads the secondaries slightly while keeping the leading edge tight against the flanks and covered with the upswept flank feathers. The young then slide down into the space under the wing and are held there by the pressure of the adult's wing. If, after climbing actively a minute or two, the

young birds were unable to reach the back of the duck, they settled and rested or slept on the floor under the duck's wings. In the wild they must attain their goal before being fatigued, or they would die of cold.

Occurrence: Climbing-up movements were seen whenever the chick was presented with an object. They climbed out of the water pan, up on bedding, and over each other. Each bird used this pattern many times a day, hundreds of times when several young huddled together.

The head movements were sometimes seen when the bird was held in the hand before feeding, but they were not a part of the feeding response. They were a result of a climbing reaction triggered by being picked up or disturbed, but there were no climbing movements of the legs at the same time. Head movements were much more prominent when the bird climbed something large, and were often not seen at all when they climbed over each other.

Species variation: Lateral head movements associated with climbing-up were common in Western and Red-necked Grebes on the first day, the amplitude being greater in the Western Grebe because of the longer neck of this species. Some Eared Grebes used lateral head movements; others did not. They were not seen in Pied-billed or Horned Grebes. Western Grebes were more lethargic than the other species and climbed much less in the box. They climbed in the same way as the other species to get out of the water.

Development: Climbing-up movements were present and well-developed from hatching. The last head movements at hatching often continued into climbing movements. Head movements were seen commonly from hatching through two days, and not at all after that. Climbing-up remained the

most frequent behaviour pattern during the first 10 days, and then began to taper off. The birds began to swim voluntarily in the water at between eight and ten days, but only for a few minutes at a time. As soon as the feathers became a little wet, they climbed out of the water onto the observer's hand or sought the other birds and climbed on them. One Pied-billed Grebe continued always to follow the observer and climb up on her foot until the twelfth day when it suddenly began to sit down beside it. Wild siblings of this same bird on the thirteenth day followed their parent in the water for seventy minutes and then climbed onto its back for fifteen minutes. They were then in the water again close to the adult for over an hour. An Eared Grebe at 17 days climbed on my hand and continued to scramble, but when put in the water it came to my hand and rested beside it. By the end of the third week climbing was rarely seen, although it occurred once briefly in a Pied-billed Grebe at 26 days.

Eliciting stimuli: Climbing followed overtaking, and the object climbed was the object overtaken. It was also seen in the nest box in a static situation. It can be divided into the climbing itself and settling or stopping climbing. Climbing is appetitive behaviour released by chilling, wetting, or alarm. Each bird acted as an individual; they did not move in a group. But on a level floor they ended up sleeping in a heap. When chilled by being put in water or in a cool or drafty environment the chick begins to call and moves around and then begins to climb anything higher than the plane it is on. The height of the object directs the climbing response. The size of objects climbed varied from small birds smaller than themselves to large slanted tables. The time in the water before climbing gradually increased. See Table VII. There were not enough observations of older birds to add them.

During the first week fear responses were not seen and all climbing was released by chilling or wetting. Then as the second down was completed and oiling became functional, the chicks swam without being chilled or soaked and the incidence of climbing diminished. However, at the same time alarm behaviour was beginning to develop, and some climbing was then triggered by alarm at sudden movements, particularly chasing. The birds never responded in this way to noises.

The releasers for settling after climbing are more complex. When the bird was chilled, the presence of warmth released settling. Softness released settling in a uniformly warm environment, and birds tended to congregate on a soft cloth flat on the warm newspaper covered floor. Reaching the top also released settling; the birds stopped climbing when they reached the top of an object and did not continue down the other side. Warmth was the most effective releaser, then reaching the top, and then softness. When climbing was released by alarm, reaching the top was the only effective releaser for settling.

Being covered was a further stimulus to settling, but probably only as it contributed to warmth. The birds did not actively crawl under or between layers, but when they accidentally started between cloths they continued to move forward.

Table VII. No. Seconds in Water Before Climbing, 8 Western Grebes.

Day	No. Observations	Range	Mean
1st	42	2-60	8.7
2nd	40	2-90	22.4
3rd	9	15-66	51.8

Comparison: In loons (Olson and Marshall 1952) climbing-up and riding on the parent's back lasted three weeks, but with increased proficiency in swimming and diving, the young became more independent and seldom rode after two weeks. Swans also carry their young under their wings, but this is not necessary for the survival of the young.

Climbing-up in loons and grebes replaces the running under and pushing up response which releases brooding in other precocial birds. The calling and appetitive behaviour of the young are the same, and the releasers for the behaviour and the warmth and softness releasers for settling while being brooded are the same. Reaching the top as a releaser replaces being covered.

Climbing-up has been adapted for escape behaviour in the grebes and replaces crouching. As in other birds it appears very early. Crouching appeared (Nice 1962) in ducks to sounds at 1-2 hours, to visual cues before 24 hours, Virginia Rail $3\frac{1}{2}$ hours, Sora Rail at 9 and 18 hours. The appearance of crouching coincided with the beginning of stage III before the young left the nest. In many species the alarm behaviour is tied to a call of the parent, at least for some days, but this did not seem to be true of grebes.

Adaptive correlates: Munro (1941) found young Red-necked Grebes dead with some damage to their necks. He speculated that adults had killed them when the young birds attempted to climb on their backs, after the young were too big for this. The decrease in climbing behaviour is rooted in the behaviour of the chicks, and would need little if any reinforcement by the adult. If adult grebes did actually damage these chicks, it would be more likely to be in connection with begging, as it continues long after climbing has stopped, and may not disappear

spontaneously. Eared Grebes (Van Ijzendoorn from Nice 1962) and Great Crested Grebes (Simmons 1955) flee from the parents after being fed. The Great Crested Grebes were sometimes aggressive toward young over a month old. Little Grebes (Ashby 1933) chased young when starting a new clutch and bit them savagely. One young was apparently killed by an adult. This was in connection with begging, not climbing.

Overtaking and Following

Problem: During the first week the chicks spend little time on the water, and a following response is not necessary. Instead the young bird overtakes its parent in order to climb-up. Then after the first week following gradually replaces overtaking, and finally at independence following disappears.

Description: When dropped into water or onto land the young bird swam or flopped-forward toward a moving object as quickly as it could, cheeping rapidly and insistently. When it reached the object it started climbing-up movements. Normal swimming and flopping-forward movements were used, but in the highest intensity.

In following the chicks swam near the parent and usually to the side or behind the adult. Neither the chicks nor the adults called or used any special directing movements. They did not follow or otherwise orient to other young.

Occurrence: Overtaking was seen regularly during the time the young were carried on the adult's back. Following developed gradually after the end of the first week, and the distances tolerated gradually increased until following disappeared at independence.

Species variation: None noted. Following not studied in the Western or Horned Grebes.

Development: During the first three days overtaking was seen in its simplest form, without any directing movements. When dropped into the water the chick swam directly forward and climbed out on whatever was in front of it. In the wild it would either fall off the nest or the parent's back and swimming directly forward either gets it back to the place from which it had fallen, or the cheeping of the chick attracts the parent. Then gradually directing influences began to be seen. The young bird stopped when dropped in the water and then overtook a moving object and climbed up.

The chicks first followed rather than overtaking on the tenth day, keeping two to four inches from a hand and occasionally dropping back a foot and then catching up. They swam only a few minutes and then climbed up on the hand and refused to follow again. At the end of the second week they followed unevenly within a few feet of the leader. By the end of the third week they followed in the water as the observer walked along the shore, but tolerated long distances, twenty feet or more. At six weeks the captive Pied-billed Grebe still returned to the observer after swimming and the wild siblings stayed near each other as they swam about.

Eliciting stimuli: Overtaking was released by chilling or alarm, and directed by a moving object higher than the water. If there were no moving object, they swam straight forward to the nearest land and climbed out; an object higher than the surface of the water released overtaking in the absence of a moving stimulus.

Following was released by a moving object higher than the surface of the water, in the absence of chilling or alarm. The size of the releaser could vary from the size of a duckling to that of a canoe, its height from a hand to a man standing upright, with no loss of efficiency.

But young grebes never followed other young grebes, and they were therefore never seen following in a line or in a compact group. They each reacted as individuals to the leader, and when there was no leader, they scattered. Calls were not necessary to release following. The distance requirements were not rigid and not related to the height of the leader. The chicks at first followed only a few inches behind the leader and if the leader swam more than a foot ahead, the chick stopped following and cheeped loudly until the leader came back within the required distance. Therefore the speed of the leader must be within the following capabilities of the chicks. On land the leader must move more slowly than on the water. Although they had ample opportunity, the grebes never distinguished one person from another in following. Fine distinctions would not be expected in animals which would follow a boat. See Table IX.

Comparison: Other precocial birds overtake the parent to be brooded when they are chilled, and the movement is released by chilling and directed by the parent to which they are imprinted. Overtaking is the predominant movement in grebes during the first week, while in the other groups following is more frequent. In ducks and other groups following can be elicited by a constantly repeated call, and the distance may be related to the height of the parent (Fabricius 1951, Lorenz 1952). The young birds often relate to each other when following and go either in a line or a close group. The duckling or galliform chick, prepared at hatching to hunt its own food, needs a highly developed following response to keep it close to the parent in a grassy

meadow or dense reed bed, and to enable the group to move to the best feeding grounds. The young grebe on its parent's back is carried and fed and its following responses are therefore simple. In ducks alarm is easily elicited and following is intensified when the birds are alarmed, even in the absence of the adult. In grebes alarm is seldom shown during the first two weeks, but when frightened the young climb on the parent's back. Later each chick dives away separately when alarmed (Table VIII). Table X shows changes in all locomotion patterns.

Table VIII. Comparison of Following

	Ducks	Grebes
Movement necessary	yes	yes
Distance related to height of leader	yes	no
Call necessary	yes	no
Any length object followed	yes	yes
Any height object followed	no	yes
Relate to other chicks	yes	no
Intensified when alarmed	yes	no

Table IX. Schematic Diagram of Responses to Chilling.

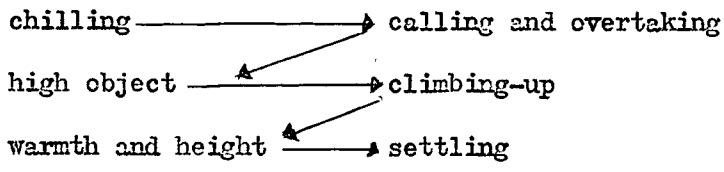
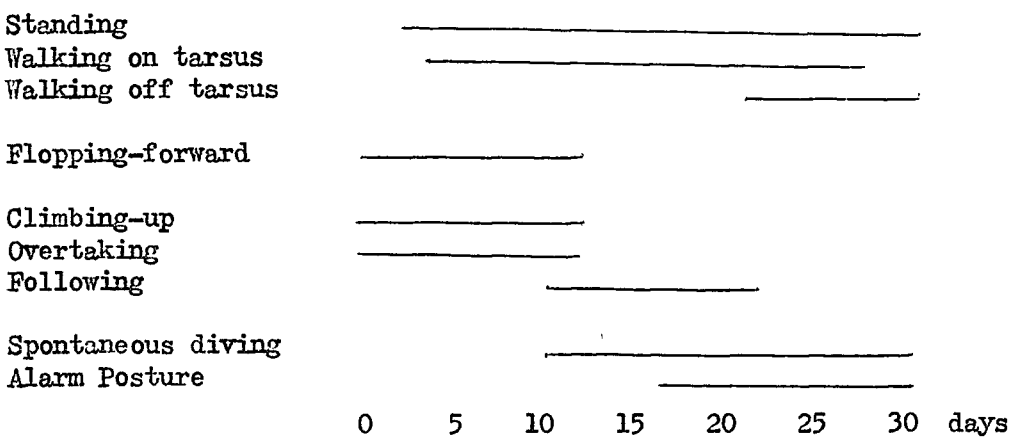


Table X. Changes in Locomotion Patterns



Flight

Description: Flight was not studied and no descriptions are available.

Occurrence: Adults migrate at night and move from lake to lake on the northern migration as the lakes open. This must involve long reconnaissance flights. During the early part of the season they move from one lake to another, and very occasionally during the day a small flock will take wing. After the first two weeks on the breeding grounds or wintering area no flight is seen.

Development: Flight does not occur until after seven weeks when the bird is fully fledged. There are no incipient flight movements, wing fanning, or practising movements. Little Grebes (Ashby 1933) flew when slightly under eight weeks of age.

Comparison: Gulls, ducks, eagles, passerines, and many other groups show incipient flight movements long before they have functional wings. This occurs in the Herring Gull (Tinbergen 1953) as early as ten days. In loons flight was achieved from ten to eleven weeks after hatching, some weeks after the full juvenal plumage was attained (Olson and Marshall 1952).

BEHAVIOUR ASSOCIATED WITH FEEDING

Begging

Description: The intensity of the begging response was directly dependent on the time since the last feeding. At the lowest intensity, when the bird was first willing to take food, it simply turned its head toward the approaching food and snatched it when it came within reach. With increasing hunger the birds began to cheep when food was seen and then when the observer appeared. The cheep was of lower intensity than the begging posture and was sometimes used when the bird was not hungry enough to bite at the food vigorously. When the birds were fed often, the begging posture itself was not seen.

When the bird was quite hungry, it began to cheep and flopped forward toward the observer begging. The neck was extended forward and then the head and fore part of the neck were raised up forty-five degrees, and held open until the food was only a few inches away. Then the food was snatched from the fingers or forceps. See Plate IV.

The bill was never held open long enough to put the food in it. It was only possible to poke the food further down the bill if the greatest speed was used. The parents hold the food still until the young bird snatches it away.

Occurrence: Begging occurred from hatching to independence at three weeks or more. Adults in captivity call when hungry and take food from the hand, but they do not use the begging posture. The young birds called to be fed about every two hours, and they continued begging at the same time interval all night if the lights were left on. If the lights were turned out, the birds slept until daylight. Grebes feed on surface

insects during the evening when it is too dark to feed by diving, but the young must fast during most of the night.

Species variation: The begging posture was very much more pronounced in the Red-necked and Western Grebes than in the two smaller species. The long necks of these birds brought the head far forward, and the head and bill angled upward grotesquely from the forward stretched necks. Western Grebes used the same posture and call, but they did not open their bills when begging. Western Grebes which had not been fed enough begged to each other and bit at each other's bills. This was not seen when they were adequately fed.

Simmons described and figured high intensity begging for the Great Crested Grebe. It was similar to that of the Red-necked Grebe with the neck awash and the mouth open showing the red interior. Simmons (1955) felt that this was used by the older young as an appeasing posture. The adults were very aggressive towards any but their mates, and he felt that this posture differentiated the chick and prevented the adult from attacking it. The chick approached the adult for food and then turned away quickly. The chicks of all species turn away when they have food to prevent other chicks from taking it from them. The high intensity begging posture was conspicuous in these older young since the adults had slowed down their feedings by this time. It releases feeding on the part of the adult, and from the present study is probably not an appeasing posture.

Development: During the first day more lower intensity forms of begging were seen. Later the high intensity forms were the more common. During the first twenty-four hours the young grebes begged to their companions, to any species of grebe, but not to ducklings. After the

first day all hand fed, captive young directed begging toward the observer's hand.

Eliciting stimuli: The most important eliciting stimulus for begging was movement. A still object was never begged to, and the still food forceps evoked no response. When these were moved, hungry birds flopped-forward and begged. A single direct forward movement was a much more powerful stimulus than a jerking movement and would elicit begging when jerking movements would not. Yet often first and second day birds stopped begging and snatched at the food as the forceps were withdrawn. Older birds were quicker to take the food. The closer the food came the stronger became the begging response and the louder the cheeping.

When two objects were presented together the smaller or more pointed one was preferred regardless of position. Touching the head or bill did not elicit begging or feeding, nor did noises or vibrations.

The begging posture was directed by the eliciting object. The head was angled to give a direct frontal impression to the feeding instrument. If the forceps were presented above the head was tilted high up. When begging to another young grebe, the head was on a level with the ground, and the neck was flat on the ground. When begging to another bird, the posture was directed to the head and bill, and after begging the chick often bit several times at the face of the other bird. These were not aggressive movements, but the movements of feeding from the parent's bill.

Conditioning developed rapidly, and within a day all birds begged when the observer appeared.

Comparison: Loons (Olson and Marshall 1952) dipped the food for

Plate IV. Begging. 1. Low intensity in Red-necked Grebe. 2. Medium intensity in Eared Grebe. 3. High intensity in Eared Grebe.

the young into the water and splashed it around several times. "In attempting to feed a captive chick, the authors found that it would take food readily from tweezers only if similar action was taken." Grebe chicks took food readily without it being splashed in water.

Feeding

Description: Food was snatched from the parent's bill or forceps with a sideways jerk of the head. It was taken close to the end of the chick's bill, and a number of forward and back jerking movements were necessary to get the piece of food back far enough in the mouth for swallowing.

A fish was usually caught or taken crosswise in the open bill and normally just behind the head. It was turned by letting it go and either catching it again as it slid around, or laying it down on the water and getting a new hold. It was then swallowed by a series of jerking movements of the head with the down movement the more forceful one. The head was held in the normal position with the bill horizontal and closed on the fish until the head of the fish was well down in the oesophagus. Then the bill was tipped up some forty-five degrees, and swallowing jerks increased in amplitude. The bill was closed on the up movement and open on the down. Six or more of the large jerks were necessary in swallowing a fish. As the tail disappeared into the mouth, the bird's head was tipped straight up for a final jerk and then lowered to the normal position. See figure 15.

Most birds shook and worried each fish and bit the head and along the back. A few differentiated fish softened by freezing and did not bite these before turning them for swallowing.

In no instance were captive grebes seen to stab food or reach for it with a closed bill. Photographs of sunfish taken from the stomachs of Western Grebes showed a hole in the center of each, and Lawrence (1950) felt that the fish had been speared. Since the birds always open their mouths to strike at food, the hole must have been made by only one mandible. Presumably the leaf-shaped sunfish, swimming vertically and turning from side to side when pursued, were too wide to be included in the gape, and were pierced by one mandible as they were caught in the opened bill. Even in aggressive movements, the grebes always bit and never stabbed. Dubois (1918) described a Horned Grebe delivering "a vicious, stinging stab", but his photograph shows the bird's bill open. In Table XII, a schematic diagram of feeding responses is given.

Occurrence: When fed all they would take at each feeding, the birds at all ages were first willing to feed an hour to an hour and a half later. Presumably this was the amount of time necessary to empty a full stomach and crop. If left alone they called loudly with hunger at two hour intervals and fed eagerly. The amount of food taken at each feeding increased gradually. See Table XI for the numbers of fish fed to one captive Pied-billed Grebe chick. An adult of the same species, captured on the northern migration and starved one day before being received by the observer, ate 1/3 of a pound of cleaned smelt per day during the first week, 1/4 pound the second week, and thereafter 1/5 to 1/6 of a pound per day. A captive Red-necked Grebe (White 1931) ate four or six 2 to 3 inch minnows per day, a Horned Grebe (Aldrich 1929) five or six 2 to 3 inch minnows per day.

Table XI. Fish Fed to 1 Pied-billed Grebe Chick.

Age	No.	Size	Interval
1 day	1-2	1 inch	every hour
3 days	2	1 inch	every hour
9 days	1	4 inches	every hour
	1	$4\frac{1}{2}$ inches	every two hours
Or	4	2 inches	every two hours

Species variation: Red-necked and Western Grebes have longer bills than the other species, and had more difficulty swallowing. Many more jerking movements were required to swallow a fish in these species than in the shorter billed birds. They also had more difficulty with sticky or dry food.

The Western Grebes were the most difficult grebes to feed. Their necks were longer and more unsteady than the other species during the first day, and later their accuracy in striking at food was not as good. In addition they often threw away food without making any attempt to swallow it. They begged to and bit at other birds, usually to the heads but very occasionally at wings or back feathers. The significance of this high feeding motivation and low feeding ability is not clear, and no observations from the wild are available. A number of kinds and sizes of food particles were offered with same results. Eventually they had to be force fed.

Development: At hatching young grebes have a supply of yolk sufficient for at least four days. Yet they beg and accept food within three hours of hatching. In the wild the young are fed as soon as they climb onto the parent's back. Some young birds were kept in the incubator tray for 24 hours before being fed, but all these died before they were

three days old. Chicks which dropped in weight more than two grams during the first two days all died before three days. During the first day the heads of the chicks were still wobbly, and efficiency in grabbing food gradually increased until at the end of the first day it was at its maximum. No further changes in feeding behaviour were noted.

Independence in feeding came gradually. A six day old Eared Grebe pecked at food dropped on the floor, but did not succeed in eating any. A young Pied-billed Grebe at five days snapped up a live fish from the floor and threw it away, but continued to watch it closely. By eleven days it followed and pecked at anything shiny. At thirteen days it begged when the author ate and pecked at things which were not shiny. Wild siblings of this bird were diving frequently at 23 days, but did not seem to be catching anything. They continued to beg to the adult and were fed eight times in an hour and a half. One dropped a fish a number of times in trying to swallow it, and each time the adult retrieved it. These birds were abandoned and feeding themselves small items of food at 28 days, but they were not seen to take any fish. The captive took food from the floor regularly from the end of the third week, but it was not until the fifth week that it was able to catch live fish in the tub.

Eliciting stimuli: Movement released grabbing responses, as has been discussed under begging. When live fish were offered to young grebes, they bit the moving fins and tail, and later they attempted to pick the fish up by these extremities. This resulted in swallowing the fish tail first. By the end of the first week the ability to turn a fish was beginning to develop and after the end of the second week fish were always swallowed head first. No experiments were made with spined fish, but turning fish developed without the stimulus of spines. Great Crested Grebes (Simmons 1955) invariably presented fish to the young head first.

Red-necked Grebes held fish crosswise in the bill behind the head and the young bird snatched the fish either by the head or in the middle, but not usually by the dangling tail. Adults always took whole fish head first, but when heads alone were given, they were sometimes swallowed posterior end first. Tails were always taken anterior end first.

Comparison: Precocial chicks which feed themselves normally fast a day or two until all the eggs hatch and they are led to food by the parent.

Loons (Beebe 1907) like grebes take food from the parent's bill. They pursued fish held in forceps on the second day, caught dying fish in the water on the seventh day, and by the eighth day caught live fish in the water. In two instances six week old loons (Olson and Marshall 1952) were fed by the parents, and these authors quote others as saying that the young were fed for a forty-five day period.

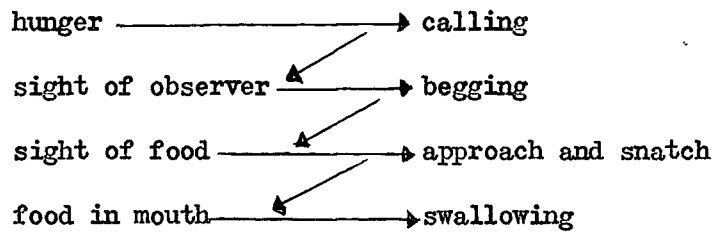
Redstarts (Ficken 1962) first swallowed moth larvae tail first. Later they swallowed them always head first. A brown spot on the head seemed to be the releaser, and unmarked larvae and pupae were taken either end first. The releaser in grebes seemed to be the hardness of the head, as it developed at the same time as the crunching and turning movements.

Adaptive correlates: Young grebes could not eat anything which was not in a firm smooth package. Turkey starter was dampened and made into small pellets, but after a few movements of the bill it became mashed and sticky and lodged in the corners of the mouth. The bird then opened its bill and shook its head vigorously. If the food did not come out, the bird bounced around head-shaking, and food adhering to the bill remained there half an hour or more. There was no bill wiping; presumably shaking the head in the water kept it clean normally.

If the food broke into pieces, the pieces were flung away with a sideways jerk of the bill. Fish which had been frozen and thawed were often mashed to a pulp in swallowing efforts and then thrown away. The only suitable food was insects and other small invertebrates, small strips of fish or meat, or whole small fish preferably fresh. Supplying food of a proper consistency was necessary, because the birds tired very quickly. After a few attempts, often only two or three, the birds rested and refused to take food.

It is well known that fur bearers cannot be fed a diet containing large quantities of raw fish, as the fish contains a thiaminase. Ficken and Dilger (1961) cited a personal communication from Dr. Robert Goodwin that Black Terns fed on raw fish developed symptoms of severe thiamin deficiency, but he does not state whether they were adults or young. Some adult birds such as penguins, alcids, loons, cormorants, pelicans, etc., subsist almost entirely on fish, and many others including grebes, herons, and some ducks have fish as fifty percent or more of the diet. Penguins and alcids feed fish to the young from the beginning. Cormorants, pelicans, and herons give a semidigested mixed diet. The others feed the young on insects, insect larvae, and crustaceans at least during the first week and then switch to fish if they are available. Grebes and ducks on small lakes and potholes where there are no fish of necessity rely on invertebrates completely. Several authors (Deusing 1939, Gross 1949, Palmer 1962) indicate that even the larger fish-eating grebes feed their young invertebrates during the first week. The author raised successfully one Pied-billed Grebe on a diet almost entirely of raw fish. The effect of thiaminase in fish must not be critical for all water birds, and it must be restricted to the first few days.

Table XII. Schematic Diagram of Feeding Responses.



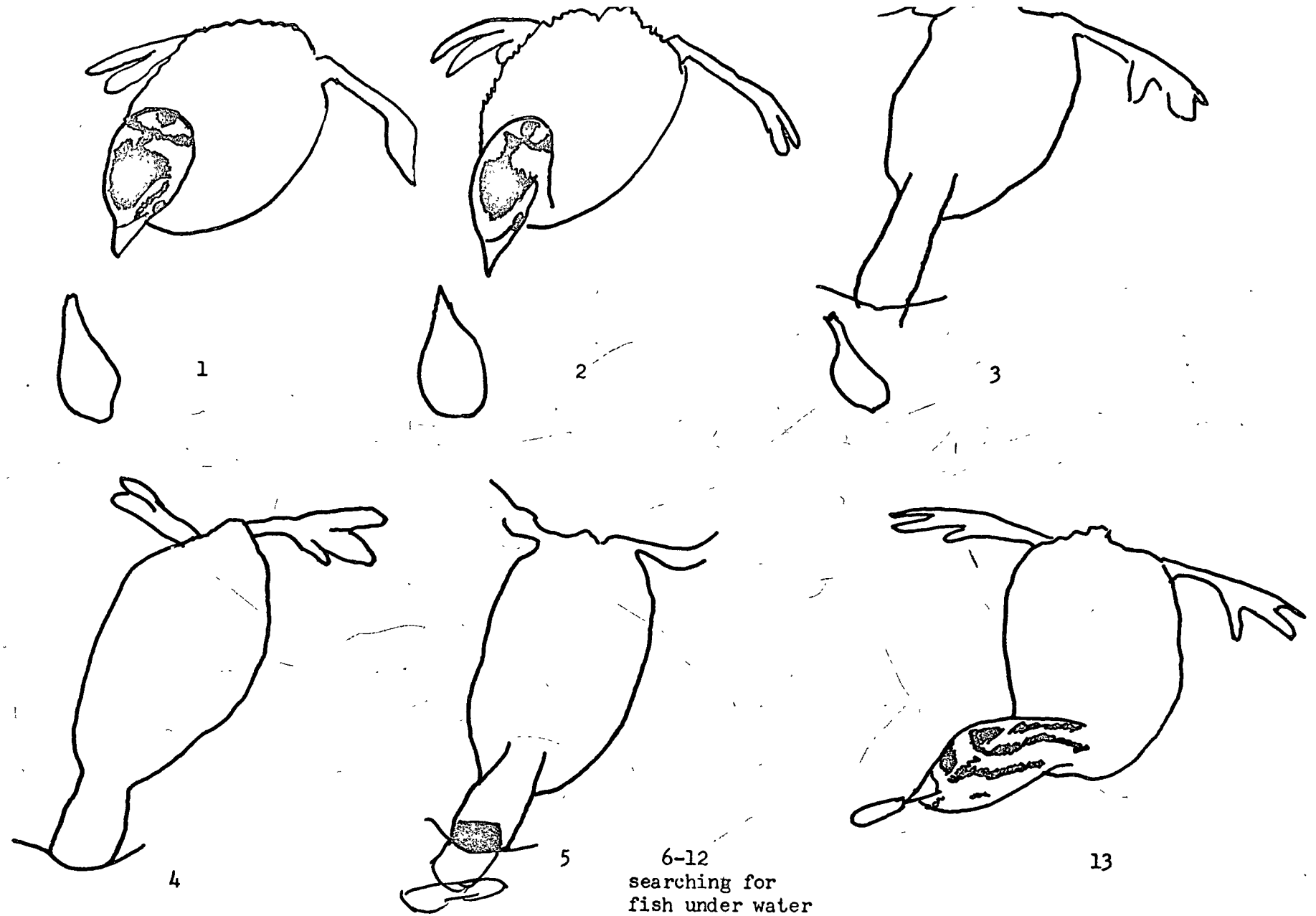
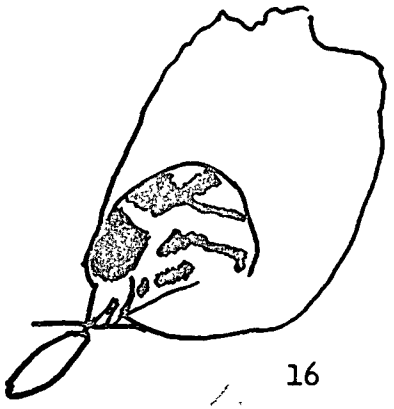


Fig. 15. Catching and eating fish while swimming on the surface.



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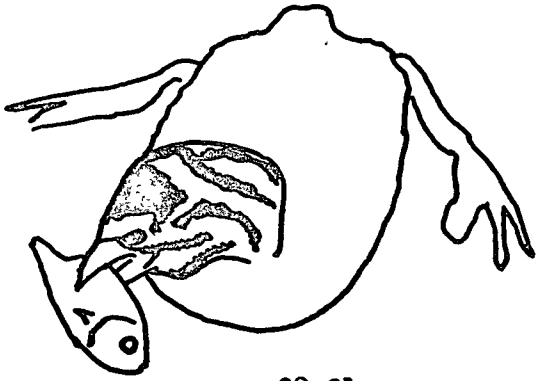

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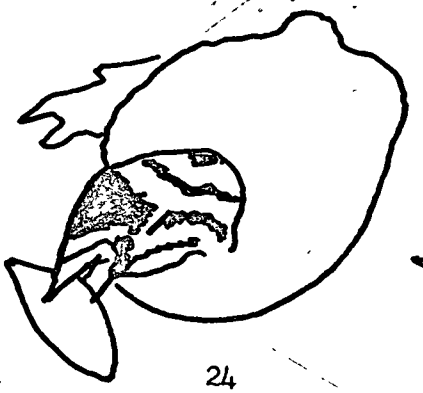

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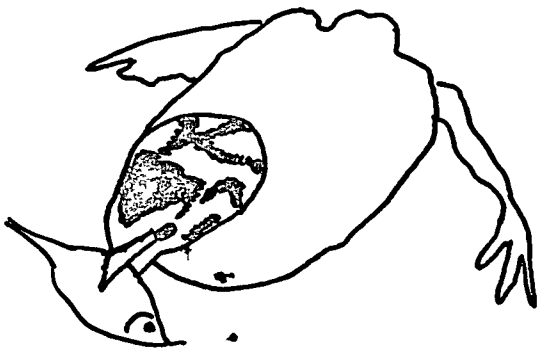

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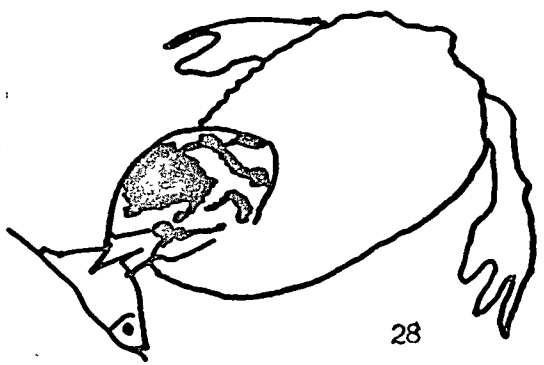

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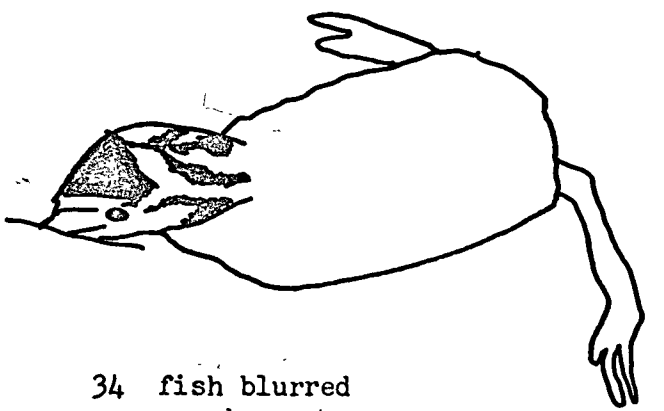
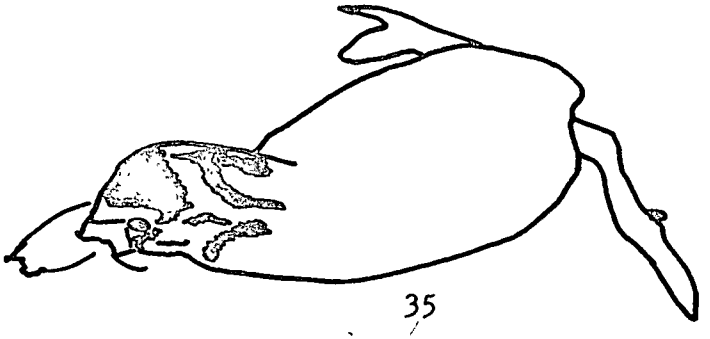


34 fish blurred under water

Fig. 15 cont.



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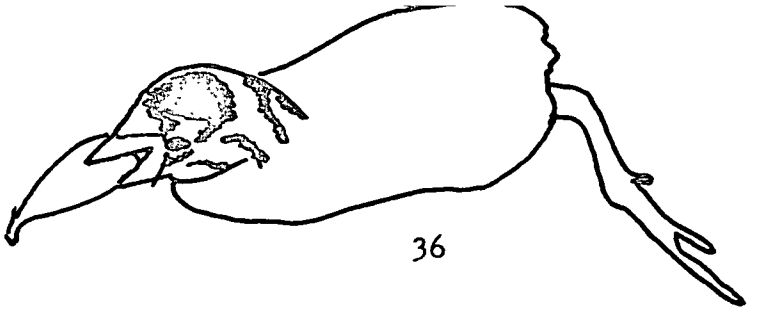

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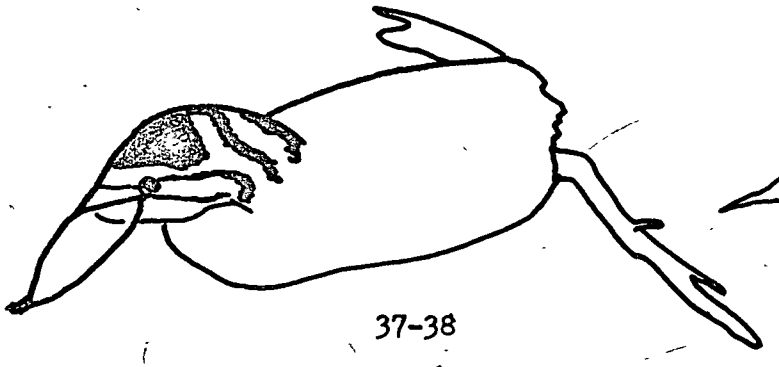

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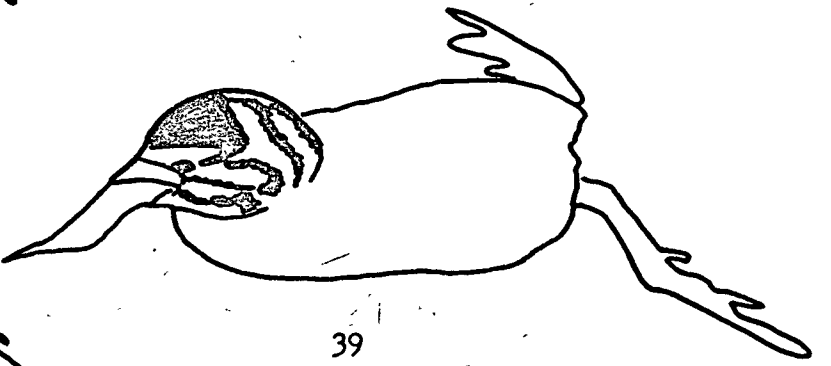

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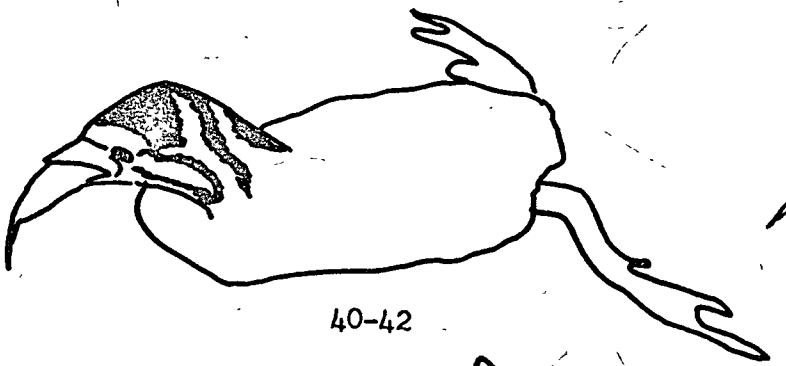

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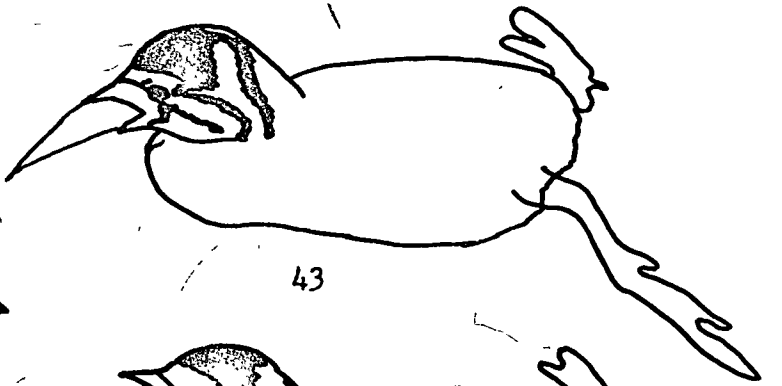

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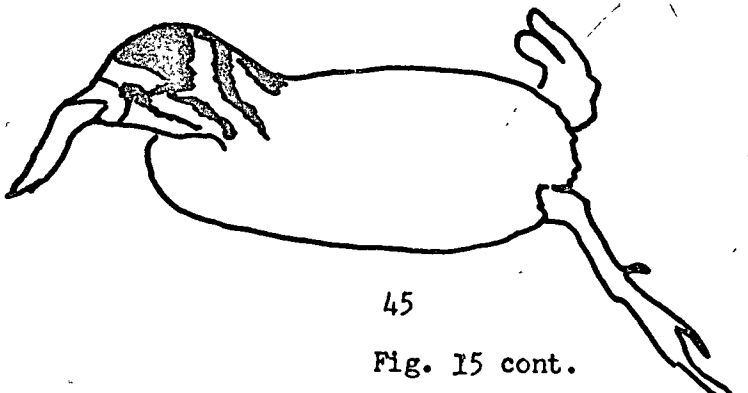

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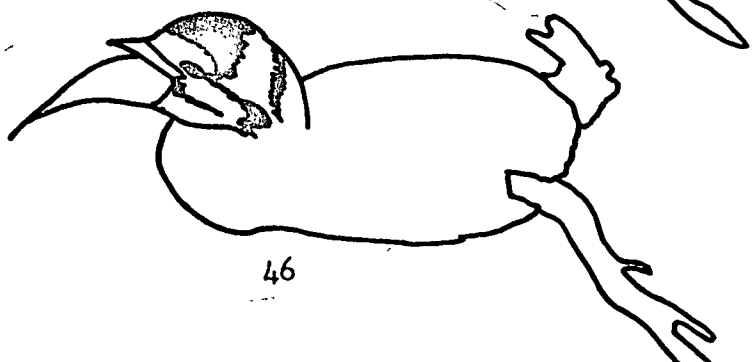

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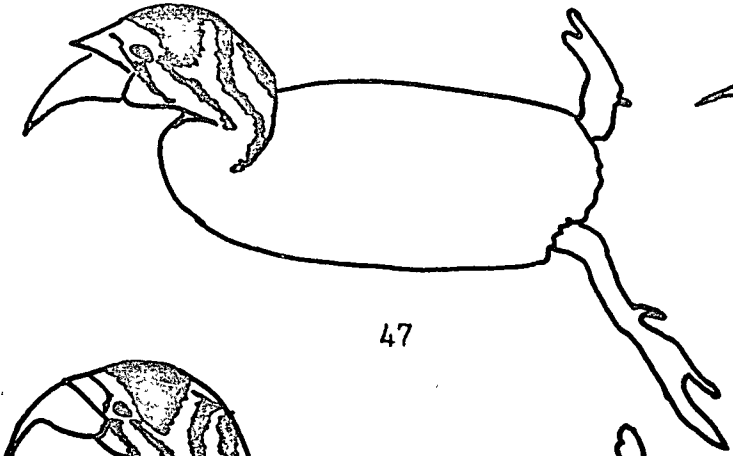

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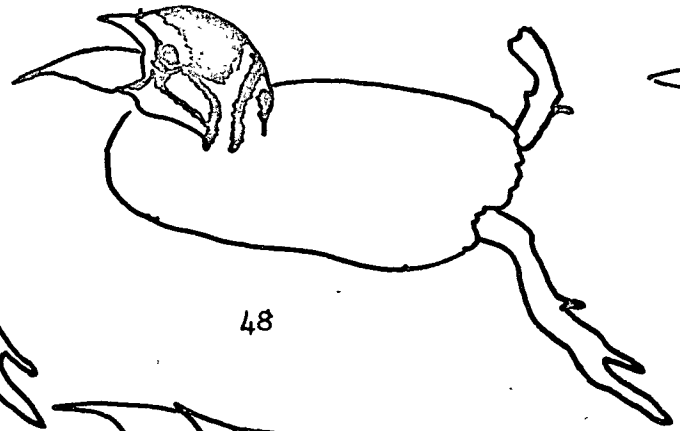

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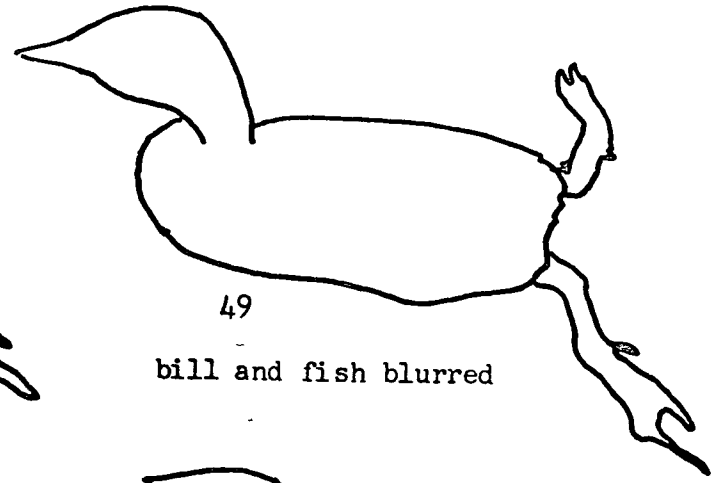
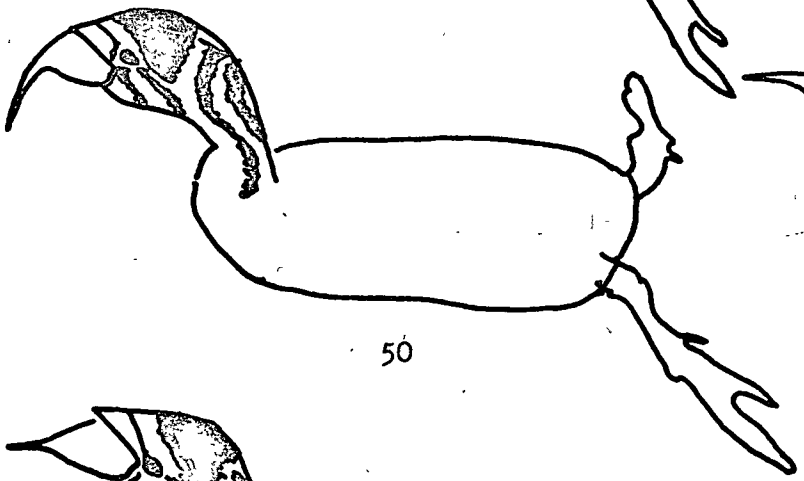


49

bill and fish blurred



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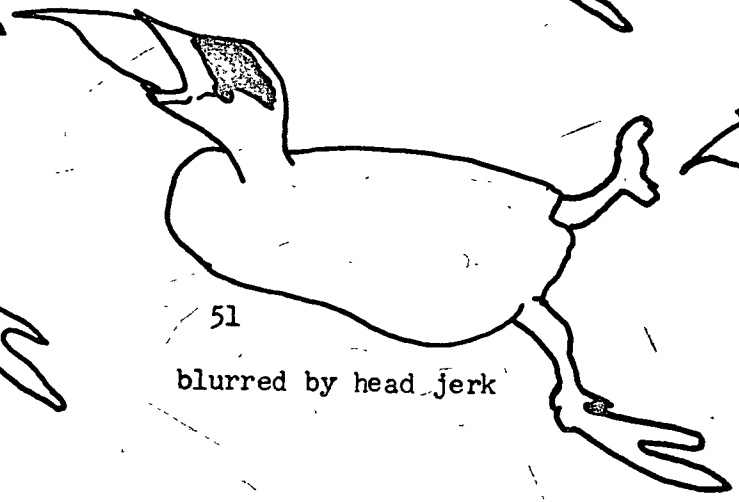
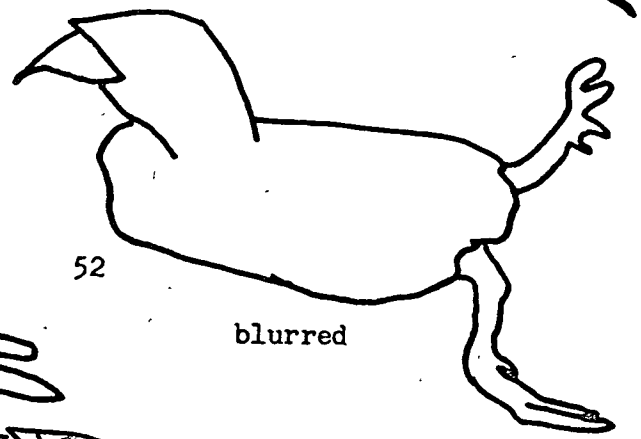


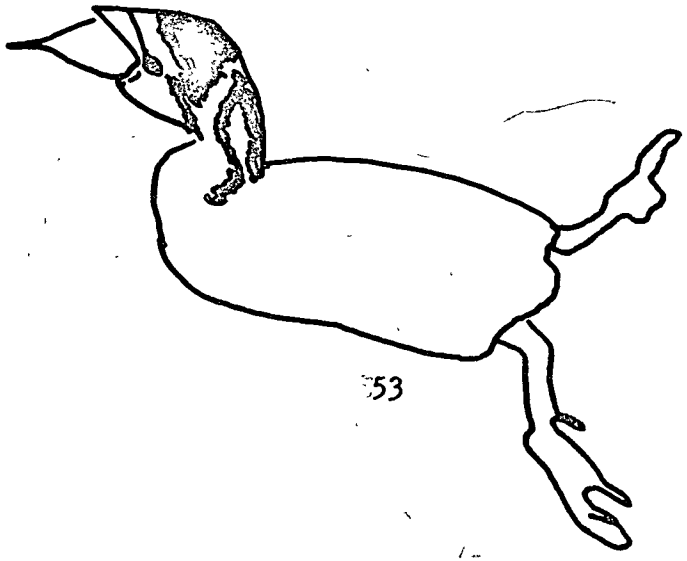
51

blurred by head jerk



52

blurred



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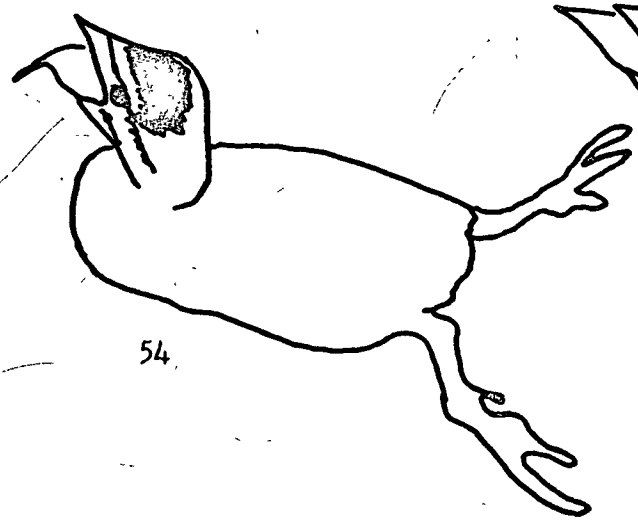

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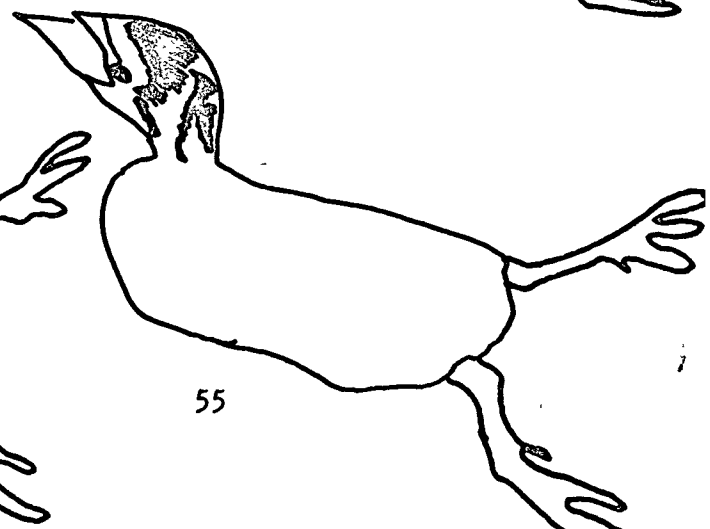

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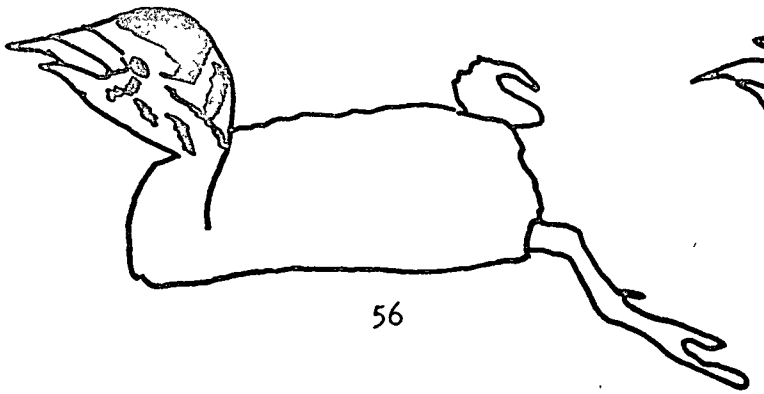
Fig. 15 cont.



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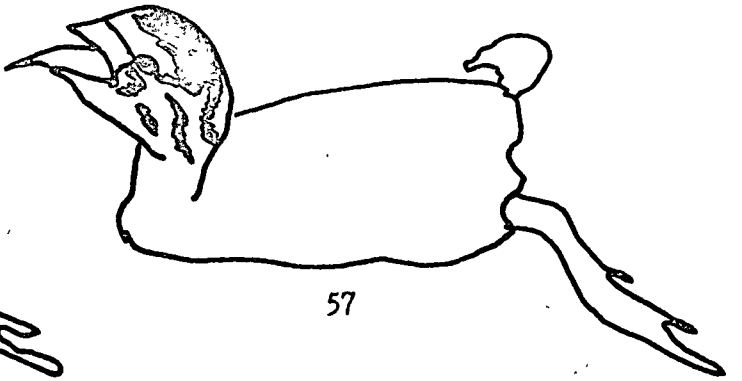
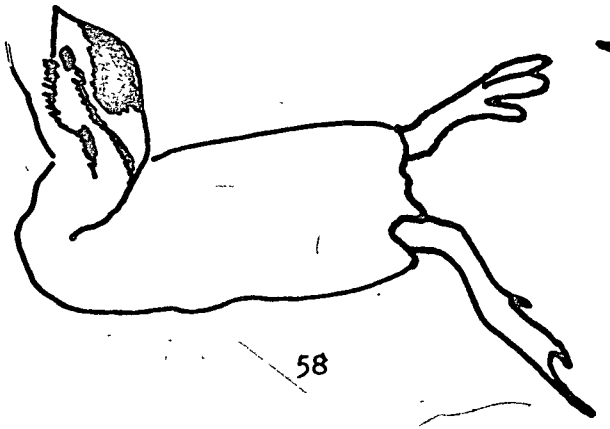


57

3 like 56 swallowing



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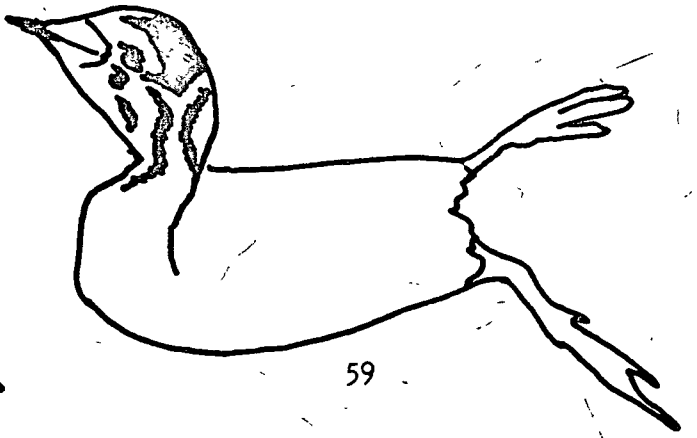


59

then head lowered to normal

Fig. 15 cont.

Drinking

Description: The head was drawn down to the resting position and the bill dipped to the water just in front of the breast (Plate I, number 10). It was opened slightly and the head was slowly tipped up with the neck still on the back (Plate I, number 12) until it reached about a forty-five degree angle from the vertical (number 11). By this time the bill was usually closed. Several mouthfuls of water were generally taken slowly one after the other in this way. Sometimes the bill was opened and closed slightly as it was being raised. The birds usually drank while swimming, but occasionally leaned over the side of the water pan and drank in the same manner.

Occurrence: Captive birds drank each time they were put in the water, every two hours. It is not known how often wild birds drink. Captives kept in the water drank every time fresh water was run in.

Species variation: None.

Development: Drinking movements were well developed and in the adult form from hatching.

Comparison: The up and down movements are the same as in many other groups of birds. Ducks mouth the water as if tasting it as they raise the bill, but this was seldom seen in grebes and then only a few times.

Feather eating

Description: Feathers were taken from the parent or picked up off the surface of the water. Adults took them as they were dislodged in preening. They were dabbled in the water and swallowed shaft first. The turning and swallowing movements were the same as those used in feeding.

Occurrence: The number of feathers eaten varied considerably. One young Pied-billed Grebe took two to six small down feathers after each meal. Captive adults which were not molting seldom loosened a feather in preening, but most that were loosened were apparently eaten. There were seldom more than two or three feathers in the tub per week.

Species variation: Feather eating was not seen in Eared, Horned or Western Grebes. No differences noted.

Development: Feathers were accepted with each meal from the first day. At first only one or two small down feathers were taken even if more were offered. The number and size of feathers eaten gradually increased. At eight days there was a sudden increase and from then on up to six feathers were taken after each meal. Begging for feathers stopped when the birds began to molt into the juvenal plumage and to eat their own down feathers.

Eliciting stimuli: In 1958 the young Pied-billed Grebes accepted feathers after each meal and begged for them after they had refused food. They begged in the same way that they begged for food, and accepted feathers offered in the same way that food was offered. There seemed to be no special releasing or directing stimuli. These birds were captured on the nest when only a few hours old, but they had probably been fed at least once by the adults.

In 1960 incubator hatched grebes were offered feathers from hatching, but they were rejected either wet or dry. Some of the birds had diets high in roughage, some low; some included fish, others did not. If feathers were force fed, the birds coughed them up. Two Pied-billed Grebes accepted feathers from the fifth day on, but two other Pied-billed Grebes, two Red-necked and one Eared Grebe raised to over a week

never accepted feathers. There was something about the feather or the way it was presented which failed to release feeding responses in the first instances. After the first times the birds presumably learned to beg for and accept feathers without special releasers.

Comparison: Feather eating is unique in grebes. Raptores, gulls, and others take in fur and feathers incidentally with their food and then cough them up along with the bones. Ducks, galliforms, parrots, and passerines eat grit or stones and use them in a muscular gizzard to grind up hard particles.

In cormorants (Van Tets 1959) the attitude used in begging for food was different from that used to beg for water. No such difference between begging for food and begging for feathers was noted in the grebes. They simply refused to take what was offered and continued to beg.

Pellet-casting

There has been considerable discussion as to whether grebes cast pellets. Wetmore (1924) described in detail the structure of the grebe stomach and the disposition of the feathers, a large ball of relatively undigested feathers in the fundus and a smaller further digested mass in the pyloric lobe. He suggested that the feathers eventually reached such a state of disintegration that they passed through the intestine. Lawrence (1950) felt that bones and insect parts were not regurgitated as they were found in the stomach in all stages of digestion. One bird had two limpet shells in the stomach which must have been there two weeks or more. Fish newly swallowed are on the outside of the stomach in contact with the digestive juices. Later they moved to the center as the feathers became entangled around projecting bones. Thus the bones were held away

from the stomach wall until they dissolved. Hanzak (1952) and Simmons (1956) both felt that the feathers surrounded sharp objects in such a way that they could be more easily ejected from the stomach.

Storer (1961) said that "the bones of most fish consist largely of calcium carbonate, which is dissolved by hydrochloric acid in the stomach but presumably not in the alkaline environment of the small intestine. Hence, it is likely that a prime function of the swallowed feathers is to retain those bones in the stomach until they can be dissolved." Simmons (1956) summarized other functions of the feathers in the stomach which have been suggested. They included protection of the stomach walls from sharp fish bones, aid in digestion, provision of vitamin D from the oil on the feathers, and use of feathers in display. The last two have been entirely discredited. There is no vitamin D in the feather oil (McKinney M.S.) and none of the observers of grebe displays have seen feathers used.

Description: Many pellets have been collected from the boxes of captive grebes, but actual pellet-casting has been seen only five times, three by the author and twice by Storer (1961). Repeated drinking preceded pellet-casting three of the five times. Then the bird opened its beak wide and drew its lower mandible back against its throat as the pellet came up. There was no choking or visible effort. The bird shook its head dropping the pellet into the water. The movement was so quick and unobtrusive that it would only have been seen at very close range. In one instance (Storer 1961) head-shaking with the bill in the water followed; in the others the birds resumed their previous activities.

The pellets collected in 1958 from a captive young Pied-billed Grebe varied in size from .3 grams to 1.9 grams dry weight. Each pellet consisted

almost entirely of feathers matted together and enclosing a few fragments of bone and chitin. The pellets were very soft and mucus-covered when fresh, and they disintegrated if dropped into water. The feather elements were clearly recognizable, not digested. The pellets dried hard and firmly molded and about 1-1½ inches long. The pellets cast in 1960 by Eared and Pied-billed Grebes consisted of bone and mucus and were somewhat smaller than those seen in 1958. The pellets seen by Storer were a green one about 3/4 inches long and 3/4 inches in diameter, and an irregular reddish pellet at least two inches long. All the pellets seen in the present study were grey.

Occurrence: Table XIII shows the variation in interval between pellets cast by one young Pied-billed Grebe. All pellets cast were recovered, and since feathers made up the bulk of the pellets, the interval depended on the quantity of feathers ingested. The diet consisted of small local fish and an occasional two inch crayfish, except during the period between June 12 and 16 when the bird ate only boneless pieces of herring. Feathers were taken with each meal.

Table XIII. Pellets Cast by One Young Pied-billed Grebe

Date	wt. grams	time	contents
May 27	.7	1 P.M.	fish fragments
May 31	.3	12-1 P.M.	—
June 1	1.3	8 P.M.	2 bone fragments
June 3	-	-	—
June 10	1.0	before 7 A.M.	5 bone fragments
June 12	-	-	—
June 19	.5	10-12 A.M.	bone fragments small
June 19	1.9	8:15 P.M.	3 small bones, 1 large and 1 small stone, head and 3 pieces chitin from beetle.
June 20	.3	-	many pieces chitin.
June 23	.3	10-12 A.M.	3 fragments chitin from crayfish.
June 23	-	3:15 P.M.	1 small stone, chitin.
June 26	.35	before 7 A.M.	1 cm. square piece chitin.
June 29	.7	3-3.45 P.M.	many crayfish chitin fragments.

The interval between pellets depends on the amount of indigestible material eaten. An adult Pied-billed Grebe kept three months was not seen to swallow any feathers, although one to three were found in the tub during each week. The bird's diet consisted of headless smelt, and for two days live minnows two to four inches long. Shrimp tails were given for several days, but the bird ate only the meat except on one occasion when it ate the telson. The telson was later found in the box not covered with feathers but presumably cast as a pellet. This was the only pellet recovered, and probably the only one cast during this period. Pellets were very soft and it is barely possible that they disintegrated so completely on being dropped in the water that they were unrecognizable, but this is unlikely in view of the almost continuous critical observation.

One Eared Grebe casting regular pellets on a fish and no feather diet stopped casting pellets when the diet was changed to pieces of lean beef and vitamins. Held on this meat diet for two weeks, it did not cast another pellet.

Species variation: Pellet-casting has been seen in Red-necked and Pied-billed Grebes and by Storer (1961) in Pied-billed and Horned Grebes. Pellets have been recovered from the box of a young Eared Grebe. Too few observations are available to ascertain whether there is any species variation, although it is not likely.

Development: A Red-necked and an Eared Grebe cast their first pellets on the eighth day while eating fish and no feathers. One Pied-billed Grebe increased its feather intake from one piece of down per meal to three or four on the eighth day and cast its first pellet on the twelfth day. Had the first two birds been eating feathers, they would have been

able to hold the bones of the fish in the stomach until they were digested, and might have cast their first pellets slightly later. There was no gradual increase in pellet size associated with increase in the age and size of the bird.

Comparison: The pellets of owls and hawks with the bones wrapped in feathers or fur are similar in construction to those of grebes. Some herons eat a great deal of vegetable matter which appears as the bulky matter of the pellets, and cormorants cast pellets encased in a mucous membrane which is presumably the lining of the stomach.

Adaptive correlates: How much of the material in a pellet is made up of food remains, bone, chitin, and incidental plant material, and how much of feathers depends on the diet. Wetmore (1924) stated that feathers occurred in the greatest abundance and most commonly in grebe stomachs containing remains of fishes and hard-bodied insects, and that they were less abundant (or were even occasionally absent) in stomachs containing soft-bodied larvae or crustaceans that were easy of digestion and assimilation. The diet of the 1958 young Pied-billed Grebe consisted almost entirely of fish from bony three inch sunfish to relatively delicately boned minnows and mud minnows (Umbra limni). The size of the fish, a consideration in the amount of bone ingested, varied from one to four inches. From 8 days the bird ate large quantities of feathers and fish up to four inches long. Before that smaller amounts of feathers were taken with 1-2 inch fish. The bones were digested and the feathers accumulated. From June 19 on, crayfish less than 2 inches long were given two or three times a day, and chitin scraps appeared in the pellets more often than bone during this period. In all the pellets the amount

of bone was only a small fraction of that consumed. The shortest time between pellets was eight hours, and during that time at least eight fish and a crayfish were eaten. In this case the purpose of the pellets was to rid the system of surplus feathers, and the bone was simply accidentally caught in the feather wads incompletely digested at the time the pellet was cast.

Feathers are not necessary for pellet formation. Storer (1961) reported that a wild Horned Grebe cast a dark green pellet after feeding on insects taken from masses of green algae. The pellet was presumably mostly algae. But when grebe chicks ate fish but refused feathers, the bones of the fish were not digested. One Red-necked and one Eared Grebe cast regular pellets consisting entirely of undigested bones, an oval mass cemented together and coated with mucus. But feathers presumably aid in pellet formation and without them pellets are difficult to cast. A number of other birds fed fish but refusing feathers were not able to cast the bones as pellets and the bones accumulated for a day until the stomach could be felt as a hard lump in the abdomen. They suddenly stopped feeding, became lethargic, and died, presumably from starvation, twelve to thirteen hours after they stopped eating. One 12 day Pied-billed Grebe managed to cast a pellet a few hours before it died, but it choked it up with considerable effort, making half a dozen choking movements and bouncing around the table. The pellet was a small one containing only about one fifth of the material in the stomach. When autopsied the stomachs were crammed with undigested bone. Why the bone did not digest in the acid environment of the stomach is not known. See Table XIV.

Table XIV. Fish and Feathers in Pellet-formation

Fish eaten	Feathers eaten	Pellets	Health
+	+	feather pellets	healthy
+	-	bone pellets	or, die, impacted stomach
-	+	feather pellets	healthy
-	-	no pellets	healthy

Summary: Pellets are cast whenever the accumulated indigestible material reaches a sufficient amount. Feathers are not necessary for, but aid, pellet-casting. Some birds were able to cast pellets without them, but others died with impacted stomachs. The feathers wrap around extending bones as the fish digests thus protecting the stomach and holding the bones together while they digest. A smaller plug of feathers prevents hard particles from entering the intestine. Where feathers were not present in the stomach bone was not digested. When the amount of feather material becomes too great, or when the feathers become too worn, they are cast as a pellet along with any other indigestible material present. Feathers, then, facilitate removal of indigestible chitin and plant material in pellets, surround hard material protecting the stomach and allowing bone to remain in the stomach until digested and prevent hard material from entering the intestine.

Defecation

Problem: The feces of grebes are almost liquid, and feathers soiled with them are no longer waterproof. It is necessary, then, that the behaviour of young grebes be adapted so that they do not defecate on the parent's back. Later spontaneous defecation replaces the earlier form.

Description: In adults and young when defecation occurred in the water, the fecal material was simply expelled. There was no movement of head or neck, or of feet. But when the adult bird was on the platform, it stood and backed up several steps before defecating. There were no accompanying head and neck movements, and the wings were not moved from the flank feathers. The few steps back served to make the fecal material clear the platform and fall into the water.

Occurrence: Young birds defecated every time they were put into water after feeding, every $1\frac{1}{2}$ to 2 hours. After the first day they defecated in the box if they were not put into water.

Species variation: Western Grebes did not stand or back up to defecate in the ten days they were observed.

Development: Newly hatched young defecated a greenish liquid mass without any special movements. They simply lay with their legs under them and wings and necks outstretched. They often defecated when offered the first meal, but when the first meal was delayed, they defecated spontaneously. This would normally occur on the nest while the bird was drying.

After the first defecation, the normal pattern was that the birds defecated explosively when dropped into the water. When the birds were put in the water for this purpose every two hours, they seldom soiled the box, and they defecated each time they were put into the water.

Spontaneous defecation was seen when the birds were not put into water at regular intervals. Under these abnormal conditions (adult grebes shake the young into the water at frequent intervals), standing to defecate, in all but the Western Grebe, was first seen 36 hours after hatching. The feet were braced about 90 degrees apart and pushed,

lifting the body up 45 degrees with the tail on the ground. There were no stepping movements, and the body was held up only a few tenths of a second. The wings were stretched out to the sides and sometimes flapped to maintain balance. If the parent did not drop the chick into the water at frequent enough intervals, the standing and flapping of the chick would tend to make it fall off the parent's back and serve the same purpose.

By the fifth day (fourth in Horned Grebes) the birds stood and backed up several steps as in the adult, and the wings were held at the sides. When water was available most of the birds scrambled into the water and defecated there. See Table XVIII.

Eliciting stimuli: In the normal stimulus situation the parent shakes the chick off its back, it falls into the water, drinks, swims, scrambles, and defecates before climbing back onto the parent's back. In this situation a number of possible releasers are present. Seven experiments were performed on eleven Western Grebes from hatching to six days of age to ascertain which of the seven possible stimuli were releasers for defecation. In the first test water was syringed over the feet, belly, and anus for 15 seconds, while the bird sat still in the observer's hand. In test 2 the bird sat quietly on a cloth-wrapped ice cube for one minute. In test 3 the birds were set on a table, where they sat still or moved around slowly for one minute. In test 4 they sat still or moved around slowly on a mirror for one minute, all attempting to drink several times. In test 5 they were set in a dishpan containing $\frac{1}{4}$ inch of water for one minute. They moved around slowly and drank. In test 6 the normal situation was duplicated by dropping the birds into deep water. They drank and swam around and then scrambled to get out. Defecation always occurred during the struggling movements. In test 7 the birds were held gently just behind

the wings so that they gave vigorous simultaneous kicks with the feet. The rest of the body was still. Each bird was tested individually out of sight of the others.

Table XV shows the results of the tests and Table XVI shows the stimuli presented in each. It is clear from the tables that drinking, contact with water, view of water, and cold are not releasers for defecation. Falling as a releaser is eliminated by test 7 and the fact that there is always a delay of 2 to 50 seconds between falling into water and defecation. The defecation is always associated with scrambling to get out of the water, not with falling in. Kicking is the effective releaser as is seen in test 7 where it is presented alone. In each of the five instances in test seven where the birds did not defecate, they failed to kick vigorously. The positive responses in tests 4 and 5 all occurred when the bird began to kick vigorously in an attempt to get out of the test situation. In test 7 in 62 instances the number of kicks was counted and found to vary between 4 and 20 with a mean of 10.8. No difference between ages was found.

Table XV. Results of Defecation Tests

test	no. trials	no. responses	% response
1. syringe water 15 sec.	22	0	0
2. sit on ice 1 min.	17	0	0
3. set on table 1 min.	21	0	0
4. set on mirror 1 min.	25	1	4
5. $\frac{1}{4}$ inch water 1 min.	20	4	20
6. set in deep water	99	79	80
7. held kicking	41	36	88

Table XVI. Stimuli Presented in Defecation Tests

test	kicking	drinking	deep water	water contact	water view	cold	falling
1.	-	-	-	+	-	-	-
2.	-	-	-	-	-	+	-
3.	-	-	-	-	-	-	+
4.	-	attempt	-	-	+	-	+
5.	-	+	-	+	+	-	+
6.	+	+	+	+	+	-	+
7.	+	-	-	-	-	-	-

+ = stimulus present in test, - = stimulus absent

In test 6 the number of seconds between dropping and defecation depended on the age and condition of the down. First day birds struggled as soon as they fell and defecated in 2 to 5 seconds. Older birds which got wet also struggled as soon as they fell and defecated within a few seconds. Dry birds swam around and drank and then after 30 to 50 seconds they struggled to get out and defecated.

Defecation in young grebes appears then to be the same response as that seen in many other birds and mammals as a result of violent action following fright or handling. This general pattern has been used adaptively in grebes to ensure that the parent's feathers will not be soiled by riding young. Defecation as a result of handling is not seen in young grebes, because they do not struggle. The same would be true of their behaviour while on the parent's back. The young are dropped into the water, struggle, defecate, and climb up again. Dropping every two hours is sufficient to avoid most accidents in the nest box. Later as the birds swim about and then struggle to overtake the parent they would defecate as a result of the vigorous activity before climbing onto the parent's back. See the schematic diagram in Table XVII.

Comparison: In a number of altricial birds the young defecate on the nest only after being fed. The pattern is usually accompanied by conspicuous movements which serve as a stimulus to the parent to remove the fecal sac. The whole relationship ensures that the young only defecate when the adult is at the nest, and that the feces are removed. Not only would feces foul the nest, but they are often conspicuous and would attract predators. In the Snow Bunting (Tinbergen 1939) and the Robin (Lack and Silva 1949) the mucous coating on the feces disappeared on the same day that the bird left the nest. Where predators are either absent, or where the nest is defended against them, there is usually no attempt to keep anything but the immediate nest clean. The young commonly squirt nearly liquid droppings over the nest rim, without an external stimulus. Kingfisher young always defecated in the deepest corner of the tunnel, then turned and pecked several times at the wall above so that dirt fell down on the wet feces. (G. Cornwell, pers. comm.). Cormorants (Van Tets 1959) always defecated downhill when on land, and when in the water they defecated and then paddled rapidly forwards.

In precocial birds the young have no external releasers or special behaviour for defecation, as they have no nest to keep clean. The adults do not defecate on the nest except accidentally as a fright reaction. Captive young rails and coots (Nice 1962) moved away from their sleeping quarters to defecate, gulls backed up several steps as in the grebes.

Table XVII. Schematic Diagram of Defecation Response

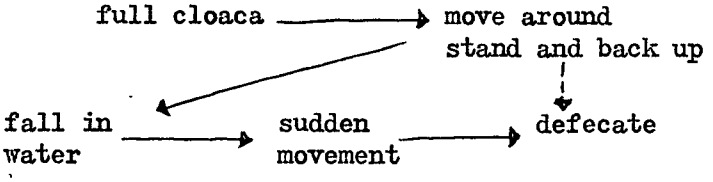
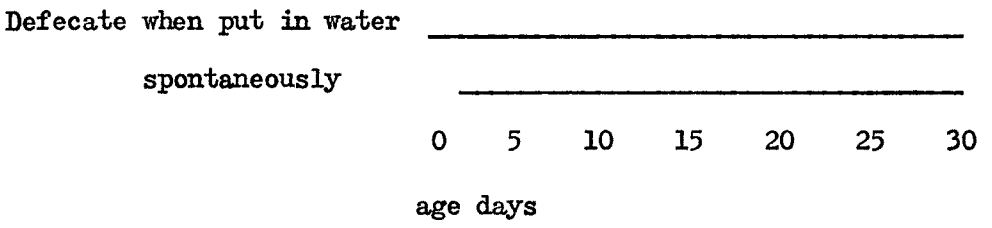


Table XVIII. Timing of Defecation Patterns



In the gulls backing to defecate appeared near the end of stage III $8\frac{1}{2}$ to 27 hours and continued well into stage V when it stopped (Nice 1962). Hazel Hen chicks backed to defecate at night (Krätzig in Nice 1962).

COMFORT MOVEMENTS

Shaking Movements

Body-shake

Description: The back feathers and wings were raised first, and the feet were paddled deep under the body until the breast rose off the water (Plate I, numbers 14 and 15). As the body reached a semi-standing position, the feet came closer to the surface and began to splash. At the highest position the head moved forward and up with the underside of the head and neck remaining parallel to the surface of the water. At the same time the scapulars rose, until they were as high as the top of the head, and the wings and side feathers were fluffed out as wide as possible (Plate I, number 16). As they were fluffed out, the head and body feathers were shaken vigorously with a rotary movement, and the head continued forward and down until the bill was plunged into the water. As the head moved down the splash from the alternately moving feet reached high over the front of the bird. As the bill touched the water, it was suddenly withdrawn directly to the normal posture. The body dropped onto the water and the feathers were snapped down. The feet continued a few fast strokes, and the bird shot forward in the water. The sequence is shown in figure 16 and Plate I, numbers 14, 15, 16. The intensity of the body-shake did not vary a great deal, but at a lower intensity the bill did not touch the water, and there was little or no splash.

Rising in the water required about half a second, extension of the neck half a second, and dropping to the water and recovery only one eighth of a second. See Table XIX for the times of body-shakes recorded on film.

Occurrence: The body-shake was done either on land or in the water. On land the feet did not paddle, and the head was withdrawn before it

dropped down towards the substrate. McKinney (M.S.) called one the body-shake and the other the swimming-shake, but there is no reason to differentiate between them; he did not differentiate between wing-shakes on land and water, and the differences are similar.

Body-shakes were done only once at a time, after each series of bathing movements, after getting out of the water, and at the end of a bout of preening. They were always followed by either a head-shake or a head-flick when they were done on the water. Rarely on land the body-shake was used during preening without the movements of the head. Preening resumed immediately, and a full body-shake was given at the end of the bout.

Table XIX. Time of Body-shakes, Pied-billed Grebe

	16ths of a second			
Rise in water	9	8	7	9
Extend bill	6	6	8	6
Recover	3	4	3	3
Steam forward	33	5	10	40
Bill-shake	2	-	2	3
Head-flick	-	2	-	-

Species variation: None.

Development: A rudimentary body-shake was seen in one Pied-billed Grebe on the second day, but in most it did not appear until the fourth day. In the one Horned Grebe a complete body-shake was seen at 5 hours, 13 minutes and regularly thereafter. It was not seen in Western Grebes until $4\frac{1}{2}$ days and only in this one instance. The movement was in the adult form, but on land only, until the birds first swam voluntarily. At first, when wet, the chicks attempted to climb out, not to shake. There seemed to be no necessity to shake for rearranging the down in the first few days. When first seen shaking

was often so violent that the bird lost its balance and fell on its side, by the sixth day, when standing balance on the tarsi was good, the tendency to fall disappeared.

Comparison: In the Anatidae (McKinney M.S.) the body-shake began with and usually ended with a vigorous tail-wag. The tail is not wagged separately in grebes. The shake then moved forward to the wings, vibrated rapidly as in the grebes but without taking them out of the flank feathers. "The wing-shaking dies down, the head is lifted from its normal position and is rotated around its long axis several times while pointing upward to make an angle of about 45° with the ground. During the head movement, the feathers of the back, neck, and head are erected. A secondary wing-shaking may occur while the head is being moved. The head then returns to its normal position, and the feathers all over the body are depressed to the usual resting stage..... The whole movement takes a few seconds to perform, the longest part often being the introductory tail-wag." In the grebes the whole movement was compressed into little more than a second, and the wing movement did not subside before the head began to move upward. In the Anatidae there were differences between species in the position and movement of the head due to the differences in body proportions and posture, but no such differences were seen in grebes.

The body-shake was used in ducks on land when the birds emerged from water and before and during an oiling preen, during and after rain, during feeding, and when released from handling. It was more frequently used by species which frequently went in and out of the water. The body-shake in the water was much less common than on land, and was seen during feeding, especially upending, and after landing on the water. The function as in grebes was apparently to remove water from the feathers, especially on the breast. In the Anatidae wing-flapping was much more commonly used for this purpose.

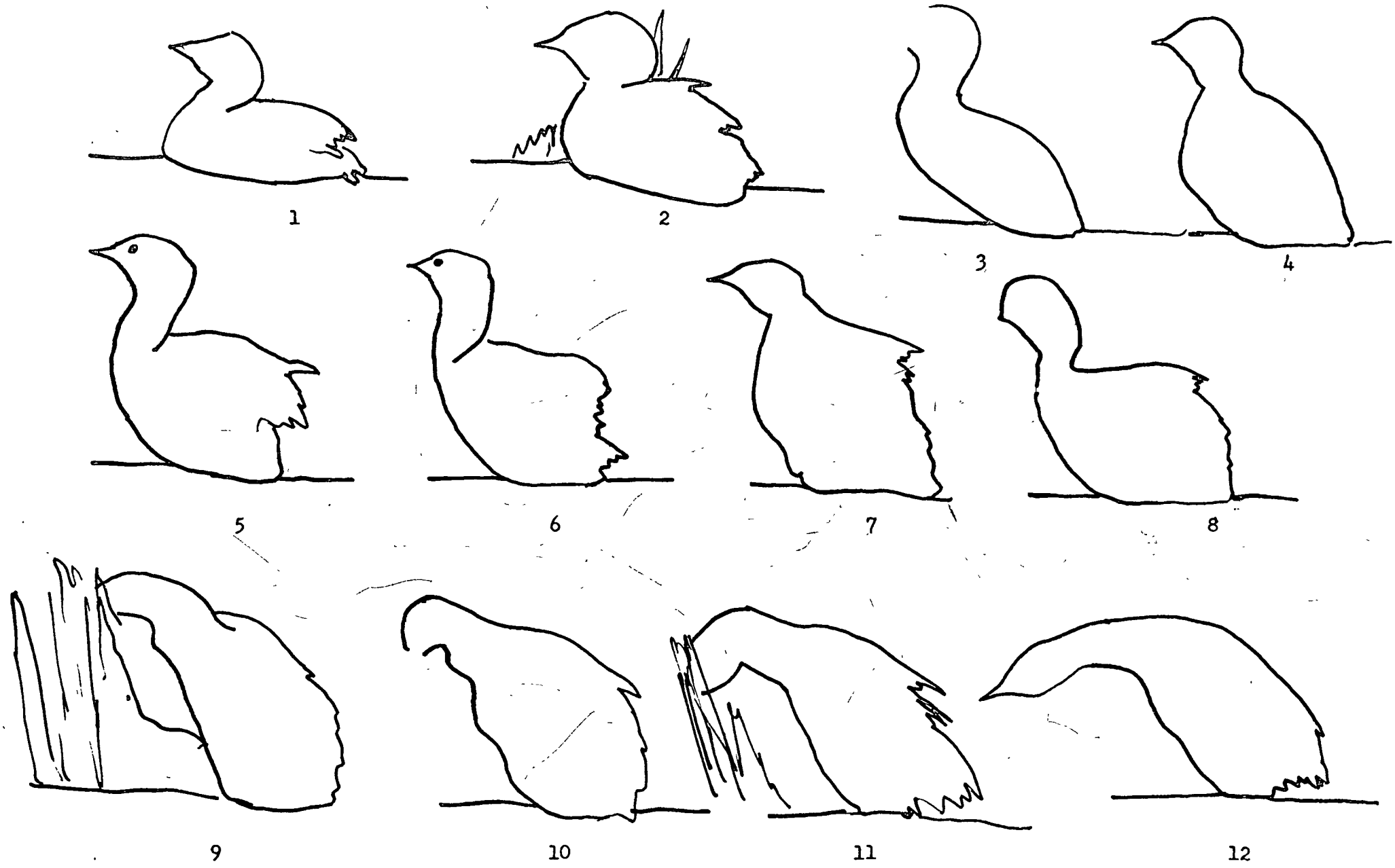
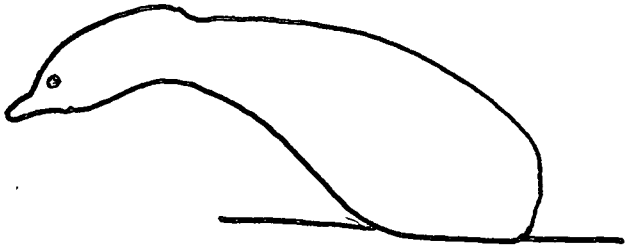


Fig. 16. Body shake.



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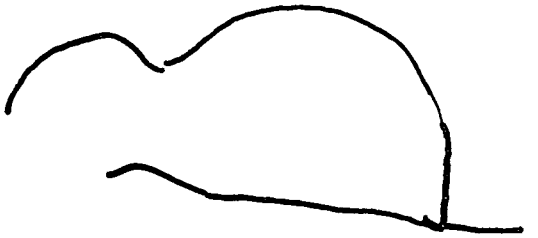

14 head plunged into water

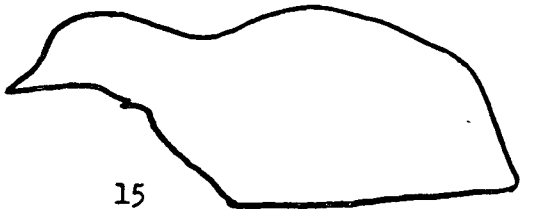

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Fig.16 cont.

Head-flick

Description: In the normal swimming posture the head began to shake in a rotary movement in a small amplitude and moved forward and up until the bill was almost straight up. Still shaking, the whole head and neck tipped forward slightly to forty-five degrees from the vertical, and then returned to normal. There was a slight side to side movement of the bill as the head was rotated. This lateral component could be more or less pronounced or absent. Head-flicks were recorded in 4, 4, 7, 5, and 2/16 seconds.

Occurrence: Head-flicks were seen after body-shakes, wing-flapping, and rarely at other times when the head was wet. The more common movement in all these instances was a head-shake, and the head-flick seemed to be used as a higher intensity movement when the whole head and not just the bill was wet. Head-flicks were also occasionally used during preening after bathing.

Species variation: None noted. This pattern was not studied in the Eared and Red-necked Grebes.

Development: In the Western Grebe it was one of the first patterns to appear, often within 10 minutes of hatching. It was not noted until the end of the first week in the Pied-billed Grebe, but it may have been overlooked. The head-flick was in the adult form when first seen.

Comparison: In the Anatidae (McKinney M.S.) the movement was the same. Low intensity movements lacked the lateral component, and lateral movements seemed to be lacking in large birds with long necks. Head-flicks occurred after wing-flapping on the water, during bathing "many times during the course of a few minutes", and occasionally during feeding or preening to dislodge water or foreign material from the head.

Wing-shake

Description: The scapulars were raised and the body feathers fluffed out and the whole body vigorously shaken. There were no head movements. This is essentially the body-shake on land without the head component.

Occurrence: This movement was rarely seen during preening on land. It would be even rarer in wild birds which do most of their preening on the water. To shake the body successfully on the water it is necessary to raise the body off the water and do a full body-shake. Even on land the full body-shake is much the commoner movement in grebes.

Species variation: None noted. This pattern was seen only a few times.

Development: Not noted in birds less than two weeks old, but may have been overlooked.

Comparison: In Anatidae (McKinney M.S.) the movement is the same, except that there may be a tail-wag. The wings (secondaries mostly) were shaken more vigorously than in the body-shake, always on land, and faster in smaller species. It occurred typically once or twice during the first few minutes of oiling while the oil was being distributed over the feathers, and it was associated with rolling the head over the wings, presumably to maintain an even distribution of oil. The typical wing-shake looked different from the body-shake, but there were intermediates.

Head-shake

Description: The position of the body and the feathers remained the same as in the last preening movement; the bill was brought to the front. This was a completely lateral movement of the head extending in the simplest instance from front to one side very fast and then more slowly

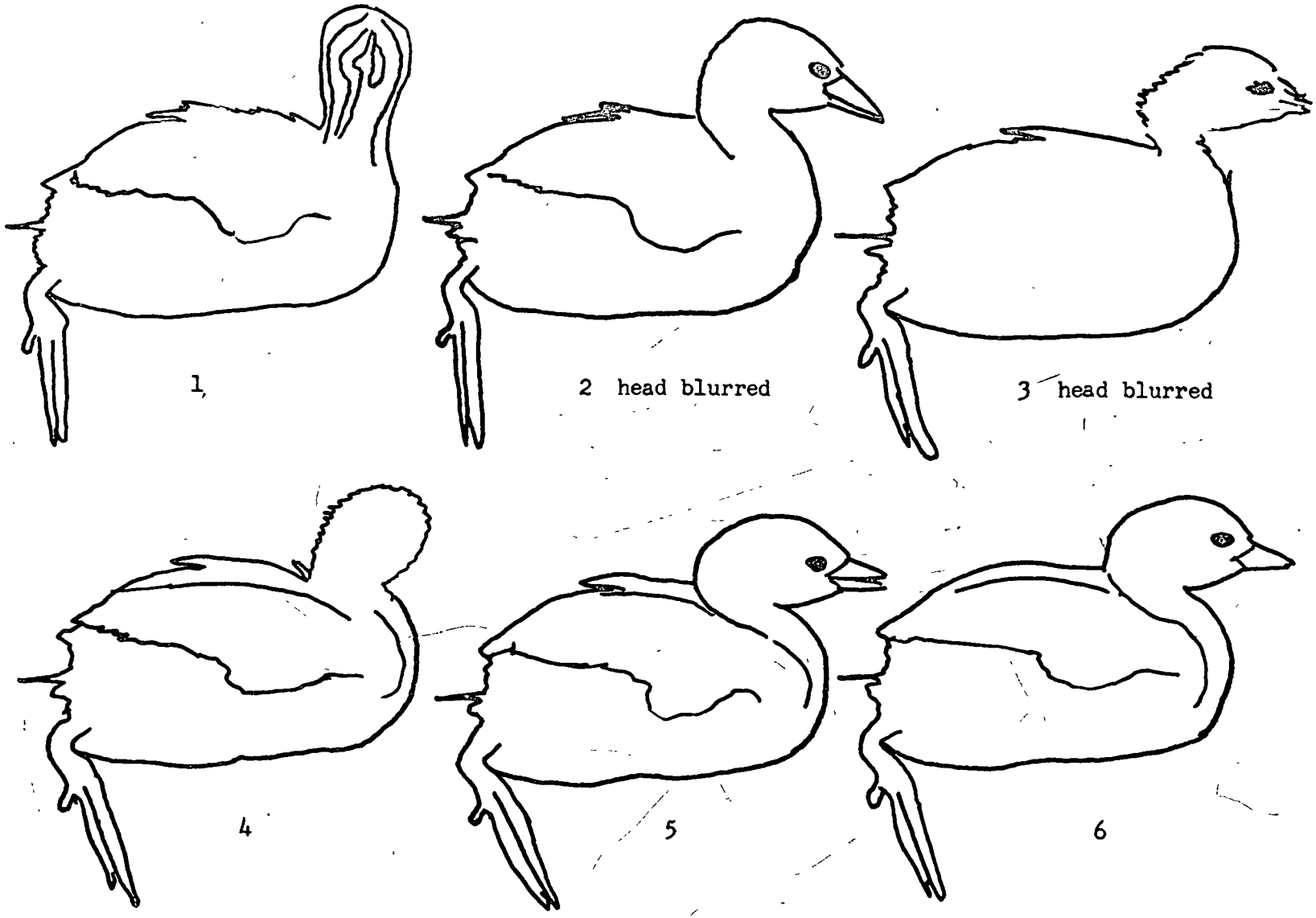


Fig. 17. Head-shake.

to the front again. The bill was usually open and any water present was flung two or three feet with considerable force. Occasionally a number of turns of the head from side to side were involved, but they were always so fast that they blurred on the film and the number of movements could not be counted. Head-shakes have been recorded as occurring in 4, 2, 2, 2, 2, and 2/16 seconds. See figure 17.

Occurrence: Head-shakes occurred commonly during preening after bathing or during preening at other times when the feathers were wet. Either a head-shake or a head-flick followed every group of preening movements, the typical form being preen+short pause+head-shake+long pause+preen. It was very rarely seen when the preening bird was dry. It was also seen after swallowing food, after body-shakes and wing-shakes, and whenever foreign matter clogged the bill.

Species variation: None.

Development: Head-shaking was present and functional from a few minutes after hatching for removing food and water from the bill. It did not develop its association with preening until preening was well established on the fifth day.

Comparison: In the Anatidae (McKinney M.S.) the movement was the same and used in the same situations.

Tail-wag

Description: Not seen in grebes. The tail is a small tuft of soft feathers which are shaken in the general body-shake but not separately. Captives whose feathers were not in perfect condition dragged their tails

in the water, but they made no attempt to get them out, and did not shake them when removed from the water.

Comparison: In the Anatidae (McKinney M.S.) tail-wags "normally follow every activity which involves, or could involve, wetting of the tail". Tail-wagging may be given as a direct response to water on the tail, but more often it is "linked in sequence with another activity and occurs even when the tail is not wet". He felt that perhaps the movement served to rearrange the tail feathers and coverts, to reinvert the cloacal lips after defecation, and he quoted a suggestion that during oiling tail-wagging might facilitate removal of oil from the gland. Tail-wagging was observed neither in oiling nor after defecation in grebes.

Wing-flap

Description: The wings were lifted at the posterior and as the feet began paddling close under the body, the body was raised until vertical in the water. Then the head was thrust up and forward so that the neck was at about a sixty-degree angle and the head straight forward. At the same time the angle of the wings was lifted, and the wings were spread and vibrated holding the body in an upright position with the line of the belly some thirty degrees forward of the vertical, about the same balance which was maintained when standing. Flapping was continued in this position up to half a second (Plate I, numbers 13 and 17). Then the wings were held spread while the body dropped back on the water. The rear border was lifted high, the wings were folded and dropped onto the back. When doing this on land, the bird remained in a standing position while the wings were closed. The sequence is shown in figure 18.

Occurrence: Wing-flapping always ended bathing or a prolonged bout of preening. In these conditions it presumably rearranged the wing and back feathers. It was usually seen only once a day in captive adults, slightly more in young. Occasionally two or even three wing-flaps were done in sequence. Wing-flapping was seen much oftener when wild birds were resting on rough water. Each bird here may flap twice or more in an hour to shake the water from the wings. It is followed about half the time with a head-shake or head-flick, presumably when the head or bill is also wet.

Species variation: Western Grebes often struck the water with the wings while shaking them, but the wings were clear of the water surface in the other species.

Development: Wing-flapping was first seen in a Horned Grebe (not standing) at 1 hour 55 minutes, and in a Pied-billed Grebe only 15 hours old, but it commonly did not appear until the fourth day. It was first seen in the Western Grebe at six days. The movement was in the adult form from its first appearance, except that in the first day or two after hatching the bird could not maintain a standing posture while wing-flapping on land. Wing-flapping on the water was not seen until voluntary swimming and bathing were established.

Comparison: The movement was the same in the Anatidae (McKinney M.S.), but it was usually followed by a tail-wag as well as a head-shake or head-flick and occasionally a both-wings-stretch coincided with the tail-wag. The posture of the head varied from species to species. The frequency of wing-flapping depended on the intensity of bathing. With a few head-dipping movements only a single wing-flap might be given; with vigorous bathing they might be given for some time. The less aquatic species used wing-flapping

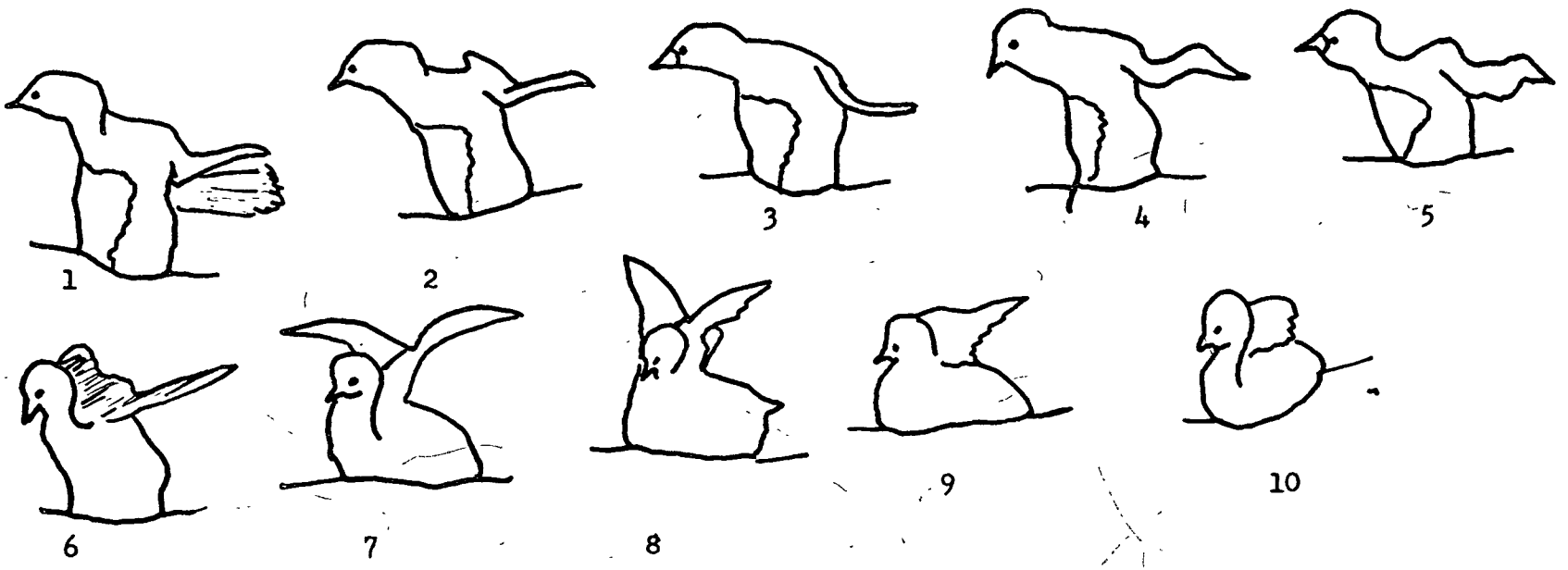


Fig. 18. Wing-flap.

more, presumably because their wings became very wet during bathing, and in this respect the grebes were like the most aquatic of the ducks. In the Anatidae wing-flaps were also seen during feeding or after sleep where they were often associated with a wing-stretch, but this use of the pattern was not seen in grebes.

In a loon (Schaefer 1955) vigorous tail-wags followed wing-flapping.

Foot-shake

Description: While sitting on the platform or swimming the birds lifted one foot out of the water at the side of the body with the tarsus and phalanges horizontal. The foot was given two or sometimes three quick flicks. In each of these the phalanges were curled somewhat to the side, the tarsus moved to the side until it was straight out, and as it moved the phalanges straightened. The foot was returned to the side and shipped away in its pocket in the flank feathers. Then the other foot was shaken and shipped. The water flicked off the foot travelled two feet or more with considerable force, and the foot appeared dry as it was put into the feathers.

Occurrence: Foot-shakes were seen before assumption of the sleep posture and occasionally during preening of the belly on the water.

Species variation: None.

Development: Foot-shaking was in the adult form from early in the first day, one Horned Grebe at 28 minutes. During the first week it was the most frequently seen comfort movement in Eared, Horned, Red-necked, and Pied-billed Grebes. As the birds slept the feet were repeatedly lifted to the back only to drop down to the floor again. After the feet could be maintained on the back, the movement was seen

only once as each foot was shipped away before sleep. Western Grebes curled the feet at the sides and made no attempt to put them on the back in ten days.

Comparison: In the Anatidae (McKinney M.S.) foot-shakes were the same except that the foot was often shaken a number of times before being put into the feathers. The movement served to remove dirt as well as water from the foot, especially when the bird was standing on land, and more shakes would be an advantage here. In grebes both feet were almost always shipped away, even when the room was warm. The Anatidae usually shook and shipped only one foot and stood on the other, and the movement was more frequent when the weather was cold.

Wing-shuffle

Description: In the resting posture either on land or on the water, the wings and shoulders were lifted alternately and quickly just enough to make a visible movement but not enough to take them clear of the flank feathers. The primaries were still and the bulk of the movement involved the secondaries and scapulars. Wing-shuffling typically lasted several minutes, and occasionally sporadically up to an hour. Each double movement took between four and five sixteenths of a second (3 in 14 frames, 37 in 167).

Occurrence: Wing-shuffles were done during a period of rest, during or after preening particularly of the wings, and after wing-stretching. It was often seen during incubation. While preening the wings wing-shuffling movements continued as the feathers were pulled through the bill.

Species variation: None. Not seen in Western Grebes.

Development: In young grebes the wing-shuffle was used from the first

day - that is, in the Pied-billed and Red-necked Grebes - using ten or more movements at a time while sleeping, this while the wings are still minute. It occurred whether or not the wings had been wet. It was not seen in Western Grebes; they allowed their wings to rest on the ground during the first ten days.

Comparison: In the Anatidae (McKinney M.S.) the primaries were fanned slightly as the wings were raised. In some species the movement began with the wings drooped to the sides and they were gradually raised to their positions on the back. When swimming or sitting on land, a grebe's wings are very close to the water or ground at rest, and it would be difficult if not impossible to extend them to the sides in wing-shuffling. In the Anatidae wing-shuffling was usually accompanied by tail-fanning, but the tail-fan was absent in the grebes.

Stretching Movements

Wing-and-leg-stretch

Description: The head was extended first, forward and slightly to the opposite side from the leg to be stretched. Then the wing and leg were simultaneously and suddenly stretched straight posteriorly. The leading edge of the wing was parallel to the outside edge of the extended leg and almost directly above it. This position was held a second and a half, and then the wing was slowly withdrawn. Both wing joints were bent simultaneously, the process taking half a second. The foot was held stationary a further two seconds, and then withdrawn in half a second to the resting posture on the flank feathers. See figure 19.

Occurrence: This stretch was used in the young about the same amount as the two-leg-stretch, once in most two hour observation periods. It occurred casually during sleep, and became less frequent as the birds became more active, until captive adults used it less than once a day. It was not associated with any other movement.

Species variation: None.

Development: Available for use, functional, and in the adult form from about two hours after hatching. One Horned Grebe used it first at one hour. Western Grebes did a one-leg-stretch between 4 and 14 hours, but did not use the full pattern until between 1 and 3 days. This use of only the leg stretch first was quite frequent.

Comparison: In the Anatidae (McKinney M.S.) the bird stood on one foot and directed the stretching wing and leg to the side. The tail feathers on the same side as the stretched wing and leg were fanned, and the feathers especially on the crown were depressed. In the grebes neither

of these occurred. In the Anatidae the foot often remains out behind and gradually drops while the wing is returned to the flank feathers, and a tail-wag usually follows. Occasionally the wing may be opened half way or less. Stretching was common in the later stages of preening before sleep, and it was usual for a bird to perform at least two stretching movements after awakening. Stretching one wing was often followed by stretching the other or by a both-wings-stretch. In the grebes the stretching movements were used much less commonly and only one at a time.

Passerines (Ficken 1962 and Nice 1943) have a one-wing-one-leg-and-tail-stretch in the adult where these three members are stretched downward and outward from the body. In the grebe counterpart of this movement the wing and leg are stretched directly posteriorly. It would be impossible for them to be stretched down from a swimming posture or while lying on the belly on land, and a directly sideways movement would be difficult to balance with the legs placed so far back. Stretching movements in passerines followed a period of rest as a "proprioceptive feedback from the muscles". They occurred as in the Anatidae in groups after resting, while in grebes they occurred singly punctuating a period of rest or preening. See Table XX.

Table XX. Wing-and-leg-stretch Compared.

	Grebe	Anatidae	Passerines
direction	posterior	side	down and to side
tail fanned	no	yes	yes
tail-wag follows	no	yes	?
feathers crown depressed	no	yes	?
foot can remain out	yes	yes	no

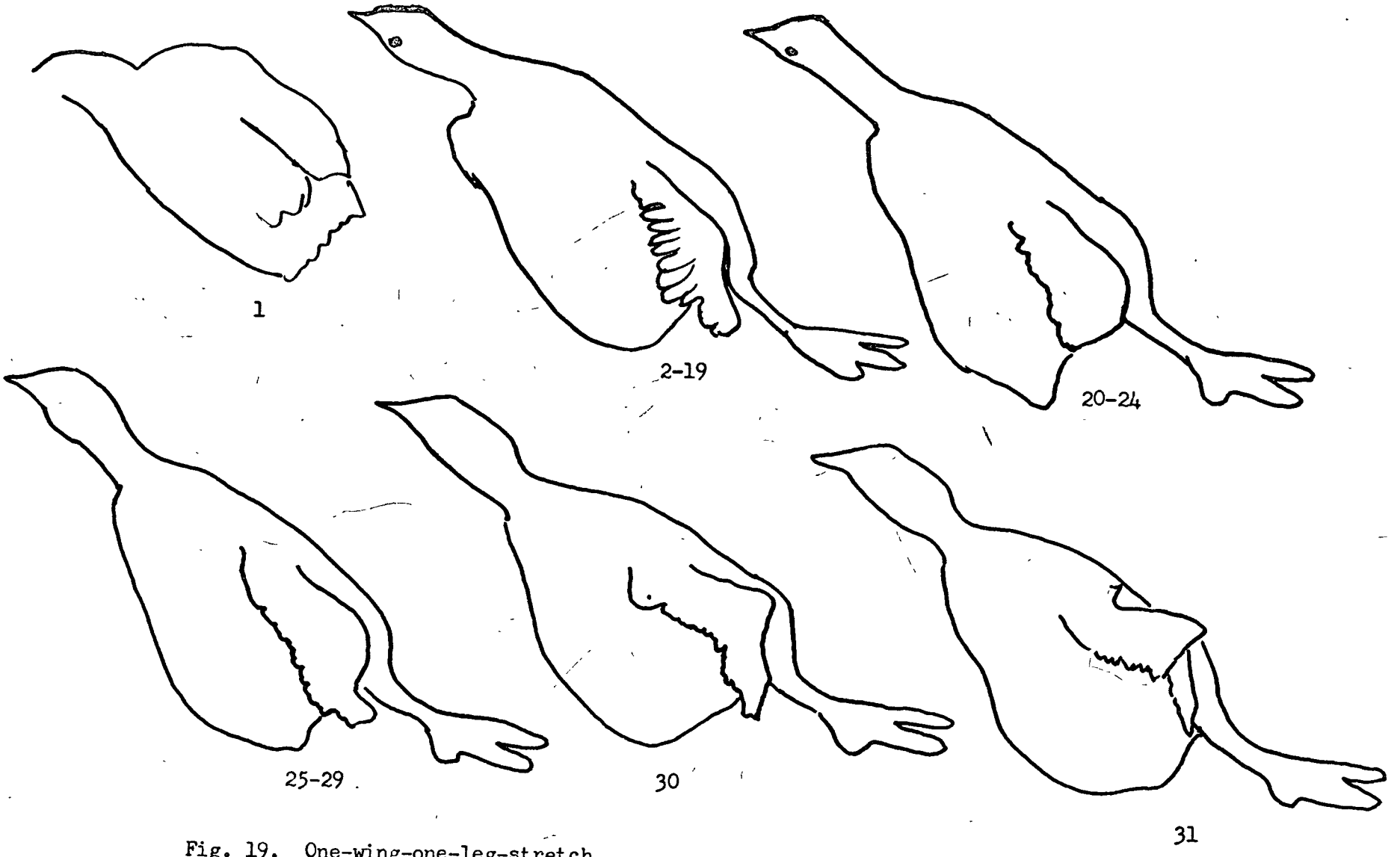


Fig. 19. One-wing-one-leg-stretch.

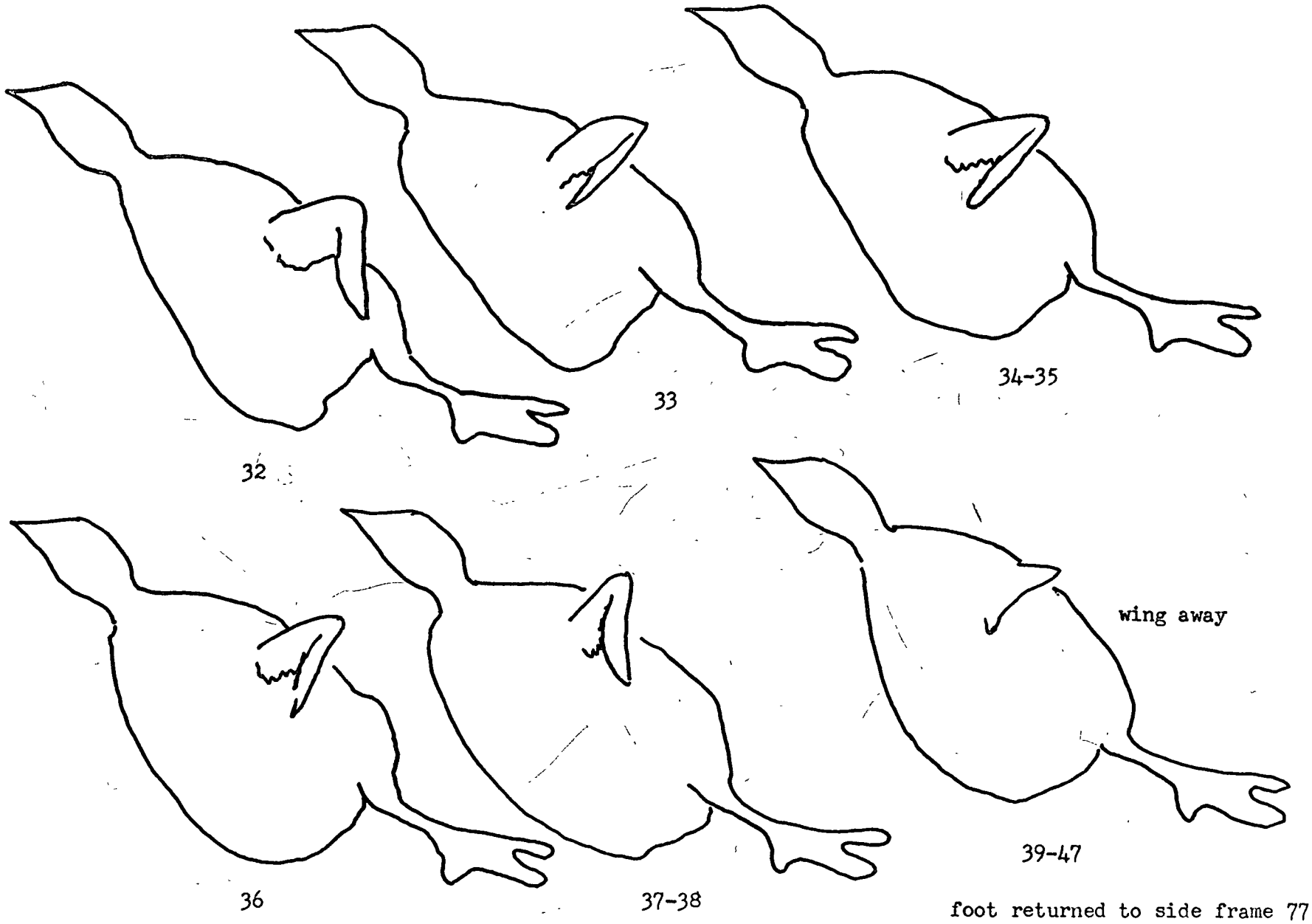

32
33
34-35
36
37-38
39-47
wing away
foot returned to side frame 77

Fig. 19.cont.

Two-wing-two-leg-stretch

Description: The neck and head were stretched straight forward with the bill slightly above and parallel to the floor. The legs were both extended posteriorly with the feet straight out behind and above the floor, leaving the body balanced on the broad flat belly. At the same time that the legs moved, both wings were stretched straight behind until the tips were over the base of the legs. Then there was a fraction of a second of tetanus and wings, legs, and head were returned simultaneously to normal. The whole movement lasted little over a second.

Occurrence: This movement occurred casually during sleep, and was equivalent to the wing-and-leg-stretch, but was slightly less common. It was not associated with any other movement.

Species variation: None. Not seen in Red-necked Grebes; apparently does not occur in Western Grebes.

Development: It was first recorded less than two hours after hatching but it was infrequent and often did not appear until the second day. It disappeared after the third day, being replaced by the uni-lateral movement. The bilateral movement may be a remnant of the stretching movements used in hatching, but it disappears later, since the bilateral movement might be difficult for an adult swimming on the water and dangerous to the eggs if done in a nest.

Comparison: A few day old Mallard duckling was once observed to do a similar two-wing-two-leg-stretch, but it is rare in ducks and lost after the first few days.

A similar temporary movement in passerines (Nice 1943) has been described. Here both wings are stretched down simultaneously. This movement lasted only two days in any one species, the eighth and ninth

in Song Sparrows; then it gave way to the one-wing-one-leg-stretch-down.

Wing-stretching

Description: Wing-stretching involved only the wings. The head remained in the normal position throughout, and in the sequence shown in figure 20 the feet remained up on the sides. The wings were lifted clear of the scapulars and slowly spread diagonally upward until the carpometacarpus was at a sixty degree angle to the radius. This position was held almost motionless for a second and a half, and then the wings were folded and laid down on the back in a quarter of a second.

Rarely the neck was stretched at the same time as the wings. Immediately after the wings were spread, the bill was extended forty-five degrees up with the occiput remaining on the shoulders. The head and wings returned to normal at the same time.

Wing-stretching differs from the two-wing-two-leg-stretch in that the wings are not stretched back over the legs but up over the back. It is the shoulder girdle which is stretched, and the wing itself is usually not completely spread. See figure 20.

Occurrence: Wing-stretching was seen about once a day per bird, during a period of resting. It was not connected with any other movement. Neck-stretching with wing-stretching was unusual.

Species variation: None noted. Not seen in Horned or Western Grebe.

Development: Wing-stretching first appeared on the first day, functional and in the adult form. Western Grebes did not use this pattern in the ten days they were studied.

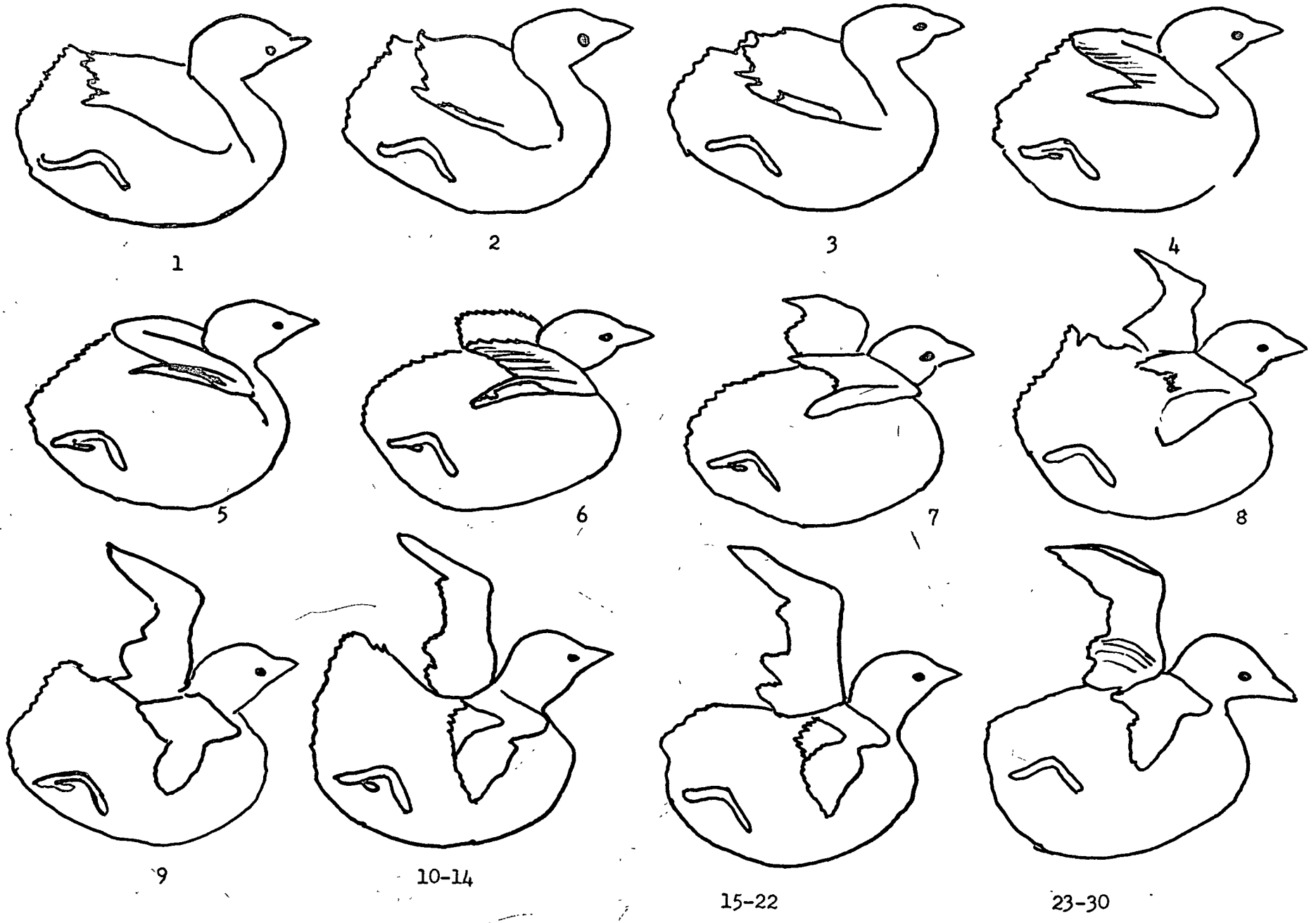
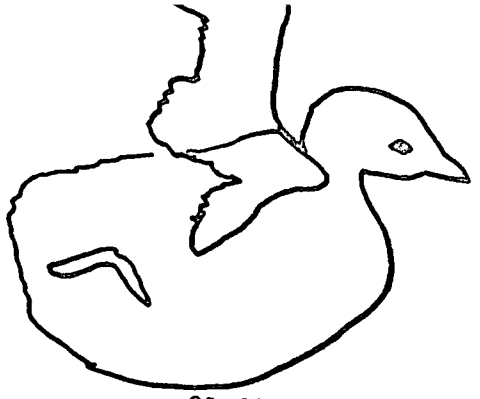


Fig. 20. Two-wing-stretch. Slightly top view.



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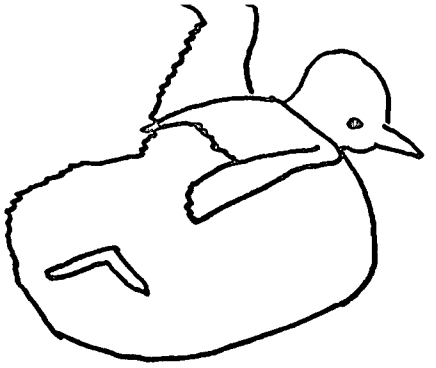

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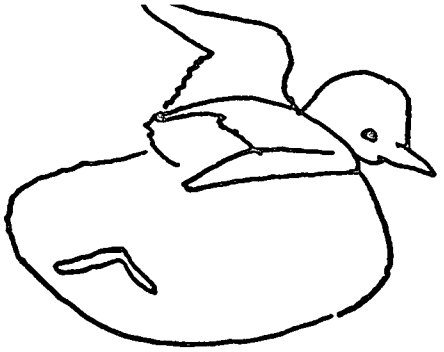

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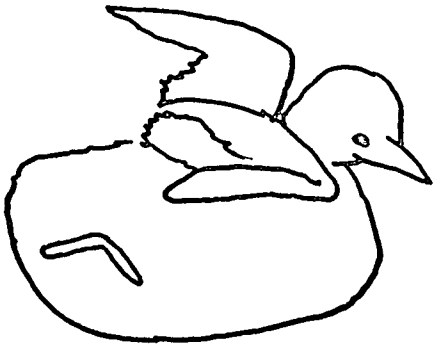

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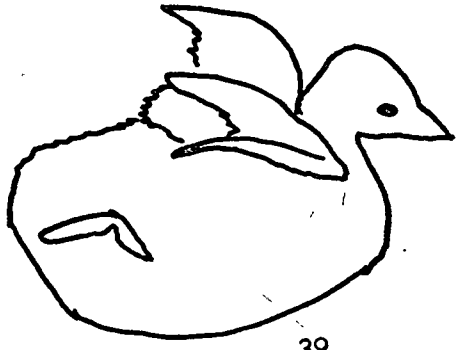

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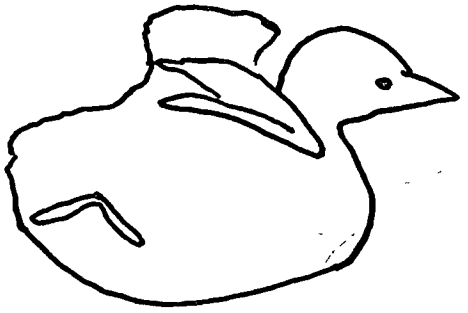

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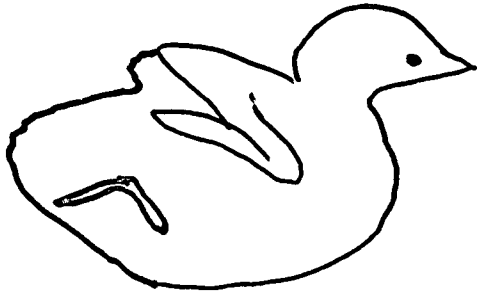

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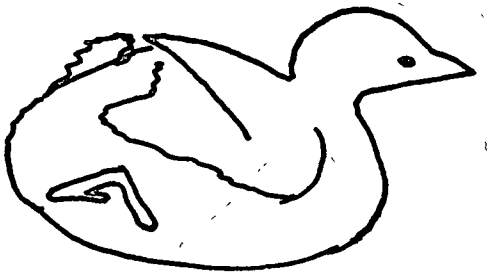

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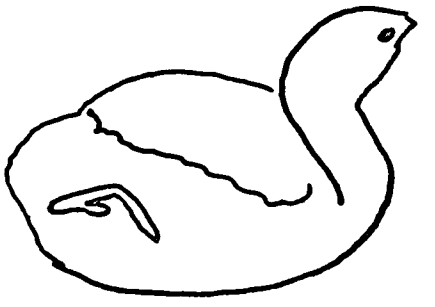

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Fig. 20 cont.

Comparison: In the Anatidae (McKinney M.S.) the wing movement is the same, but the neck is at the same time stretched forward and down with the bill more or less parallel to the ground. The feathers on the back of the neck are erected and the bill may be open. The posture was held up to a few seconds as in the grebes and then the wings and neck were quickly returned to normal. The both-wings-stretch was used in the same situations as the wing-and-leg-stretch or following a wing-flap after resting or sleep. During a series of stretches one both-wings-stretch followed two wing-and-leg-stretches one to each side.

The both-wings-stretch exists in the same form in the grebes as in the passerines. In passerines (Nice 1943) there is in addition a both-legs-stretch done on the perch. Neither the Anatidae nor the grebes have anything comparable to this.

Jaw-stretch

This movement has frequently been called "yawning", but McKinney (M.S.) used "jaw-stretch". Heinroth (1928) said that although jaw-stretching occurs in the same situations in birds as yawning in mammals, there is no marked inhalation in birds, and therefore the two are probably not homologous. There is a similar jaw-stretching movement in amphibians and fish.

Description: From the resting posture the bill was opened and the head rotated upward until the upper mandible was nearly vertical and the lower horizontal. An instant of stretching was evident, and then the head was lowered and the bill closed simultaneously. The neck was not extended and no other stretching was involved.

Occurrence: This movement was seen frequently just after hatching- as many as a dozen times in the first hour. It was rarely seen in the young after the first few hours and almost never after the third day. One adult Red-necked Grebe was seen to yawn repeatedly while incubating. This was seen by one bird on one day. Some individual young birds used this pattern a great deal, and others not at all.

Species variation: None.

Development: Present and in the adult form from within a few minutes after hatching. Nice (1962) recorded jaw-stretches in six of the eight grebes watched from hatching, at -11m, 2m, 2m, 27m, 3m, and 12m from hatching (the minus figure before hatching). It is, perhaps, a precursor to begging, but it is also seen in the Western Grebe which does not beg with the bill open.

Comparison: In the Anatidae (McKinney M.S.) the movement is the same, but it is used more. It is usually given in the resting posture and occasionally when the head was turned back in the sleeping posture, most frequently on awakening or rousing during a spell of dozing and during incubation.

Jaw-stretching occurred in the development of all groups in stage II which lasts from one to four hours after hatching depending on the group (Nice 1962). The grebes then hatch in stage II as do all the other precocial and semi-precocial birds. Altricial birds hatch in stage I and do not reach stage II for several days.

Cleaning Movements

Scratching

Description: The wing was held in the resting posture, and the opposite leg was extended diagonally to the rear. The head was turned to the side, the angle of the bill depending on the part of the head to be scratched. The scratching foot was brought forward and the phalanges extended almost straight vertically to reach the head (figure 21). The actual scratching was done with the middle claw which is larger than the others but not sharp.

Occurrence: Scratching was seen less than once a day per bird. When it occurred it consisted of three to seven movements together or interspersed with preening or occasionally as many as thirty movements followed by a head-flick. The last sequence apparently occurred when the external stimulus could not be removed for some time and the head feathers were rumpled from the scratching. The movements were regular and lasted about 3/16 seconds each (28 movements in 80 frames of film).

Species variation: None.

Development: Scratching was available for use and in the adult form from the first day. The first record was an incomplete sequence in a Horned Grebe at five hours and in a Pied-billed Grebe 12 hours old. Functional scratching movements were seen in a 20 hour Horned Grebe and in a 24 hour Eared Grebe.

Comparison: Scratching in the Anatidae (McKinney M.S.) is the same. The middle claw is modified to give a semi-sharp edge. Scratching occurred most frequently during preening and bathing, and a Mallard during a vigorous bathe lasting 5 to 10 minutes usually scratched its head three or more times. McKinney felt that scratching did not serve

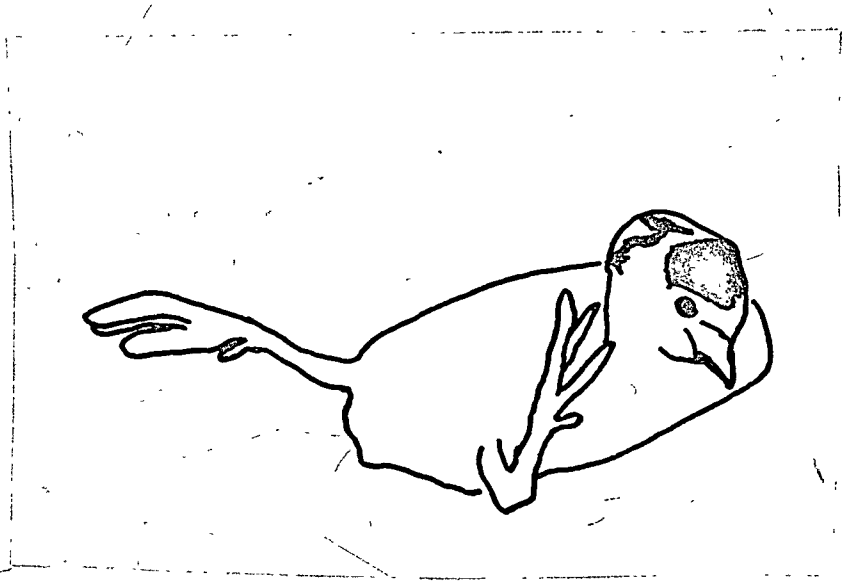

Fig. 21. Head-scratching, direct method.

to distribute oil to the head, but was a part of general cleaning movements, and observations on grebes agree.

Foot-pecking

Description: Not noted in grebes, but may have been rare and overlooked.

Comparison: In a movement similar to scratching, in Anatidae (McKinney M.S.) the foot was brought forward and nibbled with the bill during pauses in feeding or preening or sometimes during oiling. It was less common than scratching and presumably functioned as a direct response to an irritation of the foot to remove mud or grit from the webs and claws. In their almost completely aquatic existence, grebes would have little need to clean the feet in this way, and the pattern if present was not seen.

Bill-cleaning

Description: Grebes simply blew air out the nostrils to clear them of foreign matter. They did not put their heads in the water. The movement was associated with vigorous head-shaking.

Occurrence: Seen only when the nasal passages were clogged with artificial food mashes.

Species variation: None noted. Not seen in Pied-billed, Eared, and Red-necked Grebes, since these were not fed soft mashes.

Comparison: In the Anatidae (McKinney M.S.) bill-cleaning involved submerging the bill in the water and then jerking the head back slightly as air was blown out the nostrils. A series of these movements was made and then the bill was finally withdrawn from the water. Bill-

cleaning was most frequent in birds which had just awakened and it presumably moistened and cleared the nostrils. In geese it was combined with head-shaking and given during and after feeding, to remove dirt from the bill and nostrils. Grebes with their aquatic habits would have little need to clean the nostrils.

Bill-dipping

Description: Not seen in grebes, but may have been overlooked in the adult during preening on the water. It did not occur in the young or in the adult when preening on land.

Comparison: In Anatidae (McKinney M.S.) the bill was dipped into the water from the swimming posture and then raised to horizontal, not lifted up as it was in drinking. It was most frequently linked with nibbling preening in the sequence bill-dip + head-shake + nibble feathers + bill-dip ...., presumably to remove dirt from the bill or possibly to carry water to the feathers for cleaning. The usual frequency during nibbling preening was once or twice per minute. Bill-dipping was used with nibbling preening on the second day. Nibbling preening was much less conspicuous in grebes and the bill-dipping associated with it correspondingly reduced or absent.

Shoulder-rubbing

Description: From the swimming posture the head and neck were lowered to the side and turned until the right side of the head was on the right wing and the head and bill were pointing straight down. Then the side of the head was rubbed up the wing until it reached the back where the head was turned keeping the cheek in contact with the back and the white chin feathers up. The head was then snapped back to the resting posture or lowered for another shoulder-rubbing movement.

Occurrence: Shoulder-rubbing occurred frequently during oiling and bathing. During oiling two to four movements were seen, then a number of preening movements and several more shoulder-rubbing movements, perhaps on the other side. During bathing head-dipping movements alternated with head-rubbing, but as in preening two to four movements were made to one side and then a group to the other. Shoulder-rubbing served to wet and clean the head feathers and to splash water over the rest of the body. It was also rarely seen in response to irritation to the side of the head.

Species variation: None.

Development: Shoulder-rubbing was first seen in an incomplete form on the first day, but not commonly until high intensity bathing and functional preening were established. One Horned Grebe did a shoulder-rubbing movement at 22 minutes. It was seen only once in ten days in Western Grebes, at $2\frac{1}{2}$ days. It was in the adult form from the first day though not always at the first appearance of the movement.

Comparison: The movement was the same and in the same situations in the Anatidae. McKinney (M.S.) quoted Simmons (1961) as saying that shoulder-rubbing was used to clean the eye, but this was not the case when it was used in bathing and preening movements.

Bathing

Head-dipping

Description: While swimming in the normal posture, the bird threw its head forward and down into the water so that the bill touched the water with a large splash only about two inches in front of the breast. At the same time there was a simultaneous foot thrust which took the body up to a thirty degree angle from the surface and then down following the head. A second thrust as in diving carried the body below the surface, or almost so. Then the head was brought sharply back onto the scapulars and the bird rose to the surface on a slight angle at the same place it went down. There was a great deal of splashing from the sudden changes of direction. After a slight pause the movement was repeated, usually three or four times. Then there was a body-shake, head-shake, or head-flick, a longer pause and more bathing, usually of a higher intensity, perhaps with shoulder-rubbing. See Plate I; number 18 shows the raising of the scapulars at the beginning, 19 and 20 throwing water over the back with the head, and in 21 the head comes forward for the next dip. Figure 22 shows a complete sequence in an older Pied-billed Grebe chick. Timing of one bout is shown in Table XXI.

Occurrence: Captive birds did head-dipping bathing each time fresh water was run into the tank, twice a day. If they were kept out of water, they bathed every time they were allowed to swim, up to eight times a day. Grebes in the wild bathed less frequently, only once or twice a day.

Species variation: None.

Development: Head-dipping was in the adult form from its first appearance. It was not seen until the down was waterproof and the birds swam for a few minutes on the water. During the first week when the young

birds were put in the water they swam to the side and scrambled out, even before the down was wet. No bathing movements were seen on land during this period or later. From seven to ten days, the birds first began to use one or two incomplete head-dipping movements. The head often did not go into the water, and no water was thrown over the back. By the end of the second week the birds stayed in the water for longer periods and climbing-up had decreased, but vigorous bathing was not begun until after 17 days. The birds then bathed each time they were placed in the water.

Table XXI. Timing of Bathing Movements.

Dive	Recover	Shoulder-rubs	Pause	Body-shake	Pause	Head-shake	Pause
Low intensity bout:							
4	5						
5	4		8	8+6+3			
3	10						
7	44		5				
3		3,4,4					
5	24						
Higher intensity:							
4	4		46				
4		4,4,5	47				
4	4		6				
4	5						
3		3,3,4	6				
4		2	15				
4		2,3,2	8				
4		2,2	5			2	16
				10+3+3	5	2	22
						2	60
4		3,3,5	2				
3			5				
3		3,4	4				
3		3	3			2	2
3		5	6				
2		4	7			2	10
				11+3+3	2		
3		4,2	8				
4		3	6				
3		2	7			3	23
				4+3+3	18	3 flick	7
						2	

time in 16ths of a second.

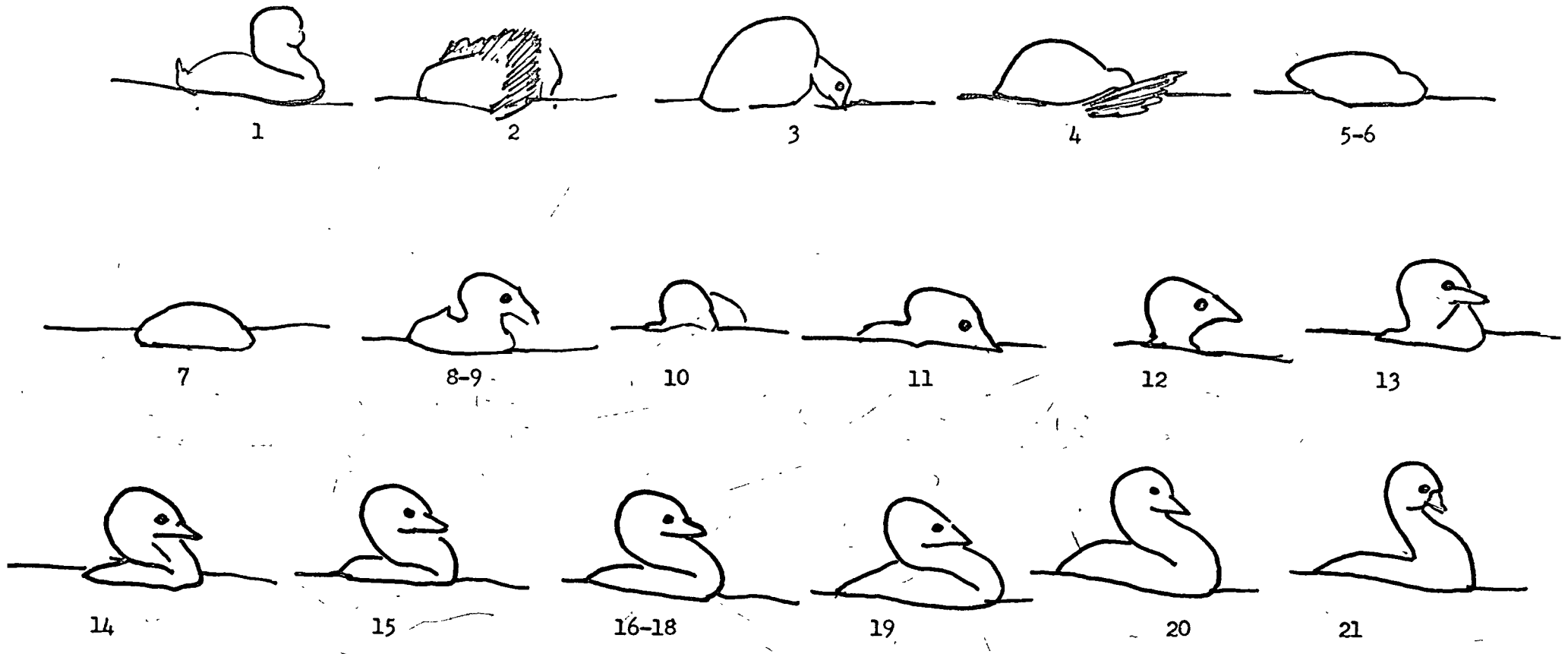

Fig. 22. Bathing, head-dipping.

The function of bathing is to wet the plumage so that it can be cleaned by preening and shaking. Young grebes are clean at hatching, and their down becomes wet accidentally probably every day. There is therefore no functional necessity for the early appearance of bathing movements.

Comparison: A comparable movement occurs in Anatidae (McKinney M.S.) where the head was dipped forward under the water and rapidly withdrawn throwing the water over the back. Undulating movements of the body followed, particularly if the bird was standing in shallow water. The grebes never bathed while standing, and the undulating movements were only one to each head-dip as an integral part of the bathing movements.

A similar head-dipping occurred in passerines (Nice 1943) as the birds crouched in shallow water. It usually alternated with a wing shaking movement.

Head-dipping was always the first bathing movement to occur in birds, and higher intensity forms appear later. Simple bathing occurred (Nice 1962) in all groups in (usually near the end of) stage IV, the locomotory stage after leaving the nest, or early in stage V. The first appearance of head-dipping in grebes was at the beginning of stage IV, but functional vigorous bathing was delayed. They fit more closely the pattern of the gulls than they do that of the groups in the precocial 4 grouping.

Head-dipping with shoulder-rubbing

Description: This is a higher intensity bathing movement. The form of the head-dip was simplified. The head was arched forward much more rapidly and closer to the water than in the head-dip alone, and the whole body was plunged under water. The bird recovered with the head on one side and one to three shoulder-rubs followed immediately. After two

to four of these sequences there was a pause with one or more body-shakes and head-shakes or head-flicks and then the bathing was resumed.

Occurrence: This pattern occurred in adults once a day or less.

Species variation: None noted. Not studied closely in Western or Red-necked Grebes.

Development: Seen at the end of the third week.

Bathing with wing-shuffling

Description: The bird drew the head and neck down on the back in a resting position and paddled with the feet. The bill was well back of the front of the breast, and the body tipped up vertically with breast and back both half submerged. The wings were shuffled alternately with greater amplitude of movement than in wing-shuffling alone, but the wings remained closed. The shuffling continued for ten seconds or more leaving the back and wings thoroughly wet. The tipped-up position was then held a second or more, and the front dropped back to the surface. Either wing-flapping or vigorous preening followed.

Occurrence: This is the highest intensity bathing pattern in the grebes. It was always preceded by the other two, and was the climax of the bathing session and the end. It occurs less than once a day in adults.

Species variation: None noted. Not studied closely in Western or Eared Grebes.

Development: Appeared after the end of the third week.

Comparison: In the Anatidae (McKinney M.S.) as the intensity of head-dipping increased vigorous tail-wags and very vigorous wing-shuffling

were added. The wing-shuffling was continuous during the head-dips but was most intense as the water was thrown over the back. While head-dips sometimes continued after wing-shuffling had begun, the more usual combination in grebes was for the head-dips to stop as the wing-shuffling began. The tipped-up posture was not seen in Anatidae.

Passerines (Nice 1943) alternately dipped their heads in the water and "crouched and performed horizontal movements with both wings simultaneously, spreading them apart and then bringing them together."

In the Anatidae there were also three other methods of high intensity bathing which McKinney (M.S.) called wing-thrashing, somersaulting, and dashing-and-diving. In wing-thrashing the bird half rose on the water and leaning to one side, beat the partly-opened wings on the surface of the water. The head was back on the shoulders with bent neck and the higher wing splashed the most vigorously, resulting in the bird's turning on the water. This may be comparable to the tipped up posture of the grebes. Their high specific-gravity would allow them to dip the tail in the water and continue wing-shuffling, while ducks would have to spread the wings and tip over to maintain their balance. In somersaulting the bird dipped breast and neck into the water and kicked vigorously in the water and then in the air as the body turned right over sideways and faced the opposite direction. Wing-thrashing followed immediately. Incomplete somersaults consisting of the first part of the movement were frequent, and the birds most likely not to complete a somersault were those with the legs spaced far apart. The grebes were not seen to do somersaults, but the intensity of the forward throwing movement of the ducks is represented in the vigorous rocking and splashing associated with bathing in the grebes. The fourth bathing movement of the ducks involved diving with the wings

open, dashing across the surface, short flights, and more dives. This was a highly social pattern, one bird stimulating others to follow. Although the grebes have a panic dive with the wings open, dashing-and-diving as a bathing movement was not seen. These high intensity bathing movements did not appear in ducks until two weeks. Occasionally Anatidae performed bathing movements on land, but this was never seen in grebes.

Wing-thrashing in Anatidae was comparable to movement three (Nice 1943) in passerines where the bird stood erect and "whipped the water forward, then backward, first with one wing, then the other, splashing the water far more vigorously than in motion one". In this case however the wings were used alternately.

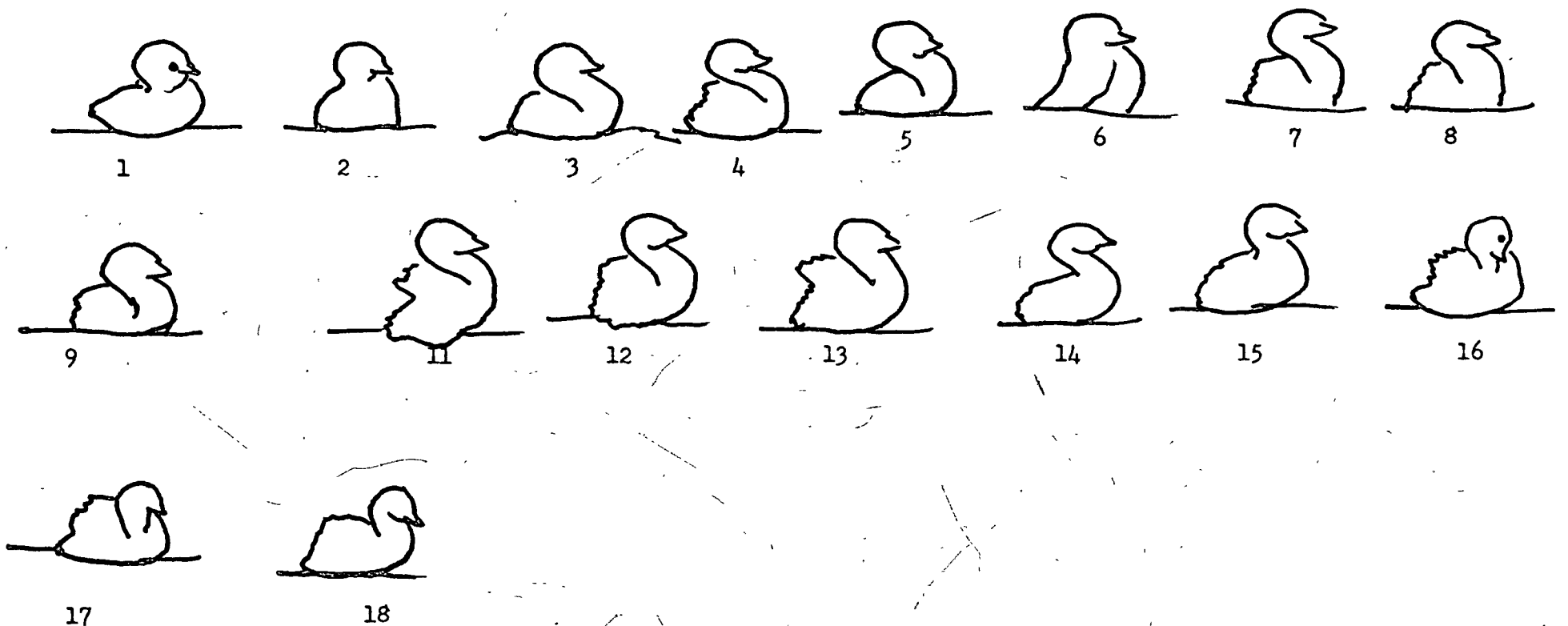

Fig. 23. Bathing, wing-shuffling.

Preening

Nibbling

Description: The bill was put into the base of the feathers and the skin or feather was gently bitten a number of times. The bill was in the feathers one to several seconds. This movement was less common than oiling preening movements, and presumably served to remove dirt and parasites from the skin and feathers.

Occurrence: Nibbling was interspersed with other preening and cleaning movements, particularly in the long preening sessions after bathing.

Species variation: None.

Development: Nibbling did not occur until after the fifth day when other preening became vigorous. It appeared in the adult form.

Comparison: The movement is the same in terns (Van Iersel and Bol 1958) and used for the same purpose. In Anatidae (McKinney M.S.) nibbling involved lateral movements of the bill and was perhaps more frequent than in grebes, but the function seemed to be the same. Nibbling combined with bill-dipping often continued several minutes.

Preening

Description: There was no special order of feather groups cleaned, but in a vigorous session after bathing the whole body was treated. Most attention was given to the neck, sides, and tail, then the breast, and least to the wings and back.

Preening was done either standing or sitting down. On land the standing position with the tarsi flat on the substrate forty-five degrees apart, and toes spread, was more common than sitting. When sitting the feet were relaxed on the substrate at the sides. In the water they were dangled in the normal position. The movements can be divided conveniently

into preening of the breast, belly, sides, and back.

When preening the breast the bird stood with its belly slightly forward of vertical (see figure 11). The feathers were all laid flat, the wings still held flat against the back and sides and covered by the flank feathers. The tail was tipped up slightly from the normal directly posterior position. The neck was contracted and the head bent down to reach the breast feathers, so that the chin was buried in the feathers being preened. The feathers were pulled through the bill and then released by pulling the head directly forward away from the body. The bill was shaken free of water after each preening movement. See figure 24.

When the belly was preened in the standing position (figure 25), the body was angled forward almost forty-five degrees, and the wings were closed but lifted free of the flank feathers. The tail was in the normal position. The belly feathers were fluffed out making a wide fringe below. The neck was arched over to reach the belly and not laid flat against the lower neck as in preening the breast. The bill was buried in the feathers about three sixteenths of a second and then pulled forward directly away from the body. When lying down the wings and tail were in similar positions as when standing. The breast feathers were fluffed out but not as far as when standing. The head was of necessity bent far to the side instead of nearly straight down in front. The foot on the side being preened was braced against the substrate or held stiff in the water to allow the bird to turn partly on its side (figure 27). The standing and sitting positions were the only ones seen in captivity. In the wild both loons and grebes often preen the belly while swimming by rolling over to one side with the upper leg extended out behind and the lower one sculling in the water. They then reach back to the breast feathers and preen them.

When the side feathers were preened, the body was forty-five degrees forward with the wings very slightly freed from the flank feathers and the tail directly posterior. The feathers were all laid flat in their normal positions. The neck was contracted and the head bent down in contact with the feathers on the side of the neck. Here it could be seen that the lower mandible was pushed deep into the feathers, and whole groups of feathers were taken in the bill at once (figure 27).

The feathers around the tail were usually preened from a sitting position. The tail was straight up to thirty degrees back, and the wings were slightly freed from the flank feathers. The head was turned to the side being preened with the bill facing straight backwards, and the twisted neck was flat against the back. The feathers were preened a second or more before the head and tail were returned to normal positions (figure 28).

When preening the secondaries, the bird held its body feathers flat but lifted the wings slightly on the back. The tail was tipped straight up. The head was arched back with the upper neck not in contact with the body. The bill was at about a forty-five degree angle from the vertical while it was in the feathers. In pulling the neck was held still and the bill tipped up in an arc until the tip of the feather slipped through it. Then the bill was returned to the feathers through the same arc. See figure 29.

For the scapulars the head and neck positions were similar to those used in preening the secondaries. The tail, however, was straight out behind. The scapulars being longer than the secondaries, the bill moved higher in its arc and was pointed almost straight up when it reached the tip of the feather. See figure 30 and 31.

When the undersides of the wings were preened, the tail was straight out, the wings slightly lifted, and scapulars lifted slightly away from the wings. The neck was not arched but laid on the back; the head could be facing sideways to almost straight down. When pulling the feathers, the neck

was still and the bill arched upwards as seen before. See figure 32.

See Table XXII for the duration of single preening movements. The length of time spent pulling the feathers depends directly on the length of the head movement required to reach the tip of the feather.

A head-shake or head-flick followed every 2 to 8 movements when the bird was wet, but did not occur when the feathers were dry. Preening movements were broken into groups of several to a dozen all at the same place. Then the head returned to the resting position for a short pause, head-shake, longer pause, then more preening perhaps in another place. After three to a dozen groups of such movements there was a body-shake. The bout ended with a body-shake and occasionally a wing-flap.

Interspersed with preening movements were those involved in oiling, shoulder-rubbing, rubbing the head on the oil gland, and nibbling the gland. The bird raised the feathers above the gland exposing it to view, then pulled at it several times with the bill (Plate I, numbers 7 and 8). The head was rubbed on the gland. The head was dropped back usually with the bill facing directly to one side. Then the bill was swung in a horizontal quarter circle until the top of the head was rubbing against the back in the region of the oil gland. The bill was then brought up to nearly vertical and to the side again. There were slight pauses when the bill was at the side. The movement was repeated two or three times and the head was returned to resting. Preening followed and later more nibbling the gland and head-rubbing usually on the other side. Shoulder-rubbing was interspersed with preening movements, but usually not following head-rubbing on the gland. Head-rubbing is shown in Plate I, number 9.

Occurrence: Vigorous preening occurred with oiling after bathing, about twice a day. A few groups of movements were seen about every two

hours, most often to the scapulars or neck. Preening was not seen during bathing, but after bathing the water was first removed from the feathers with many head-shakes interspersing the preening movements, and then the feathers were oiled and preened further. Sessions usually took several minutes.

Species variation: None. Western grebes did much less preening in the first few days.

Development: On the first day the only preening movements were single movements, unoriented and often not touching the feathers at all. These were most commonly preening the neck and wing. On the second day some of the birds stood for a fraction of a second and made single preening movements which included movements to the side and belly feathers. The pattern was complete but the feathers were often not caught in the bill. There was considerable individual variation in which movements were used, but there were never more than half a dozen movements seen in two hours, most often only one or two. Some individuals did not preen at all in the first two days, although they were active in other ways. Preening is in any case not functional at this time. A typical bout of preening in a two day old bird was one movement to the center neck, two to the right wing, and one to the right flank. Then the bird moved away a few hops and went back to sleep. See Table XXIII for the development of preening in Western Grebes.

Preening gradually increased until by the fifth day it was enthusiastic and prolonged to four or five minutes at a time. One bird showed occasional oiling movements on the fourth and one on the fifth day, and one bird did one movement only on the sixth, but oiling was not seen in most birds until the seventh day. After the sixth day the oil gland could be seen when the bird was at rest; before this it was covered with down. Hand manipulation of the gland in birds under six days showed no visible signs of oil.

Table XXII. Duration of Single Preening Movements, Pied-billed Grebe.

	No. Obs.	Bill in Feathers Range	Bill in Feathers Mean	Pulling Feather Range	Pulling Feather Mean
Neck	7	2-3	2.7	1	1
Breast	13	2-7	3.6	-	-
Secondaries	5	1	1	2	2
Scapulars	23	2-6	2.7	2-4	2.7
Under wing	3	2-6	4.6	4-6	2.5

Table XXIII. Development of Preening, Western Grebe

Age Days	Time	No.birds	No.bouts	Movements/bout Range	Movements/bout Mean	Region preened
0-1	1h	5	3	1-3	2.3	side
1-2	1h	5	9	1-11	4.1	side, neck, wing
2-3	16m	2	6	6-77	24.2	side,neck,wing,breast, back.
Functional Bout:						
$5\frac{1}{2}$	10m	1	1	370	370	side,neck,wing,breast, back, tail.

Captive young showed considerable dryness of the legs and feathers at four and five days, and when a thin coating of mineral oil was given, the condition of both legs and feathers was greatly improved. This may have been deficiency of the diet, or the wild chicks may get some oil from the parent's feathers as they ride on its back.

Comparison: Preening was similar in Anatidae (McKinney M.S.) and terns (Van Iersel and Bol 1958), but in the Anatidae preening occurred during bathing as well as at other times.

Preening is present very early in precocial groups, the first movements being seen in stage II, an hour or so after hatching. Preening and oiling are vigorous and functional from the first day in ducklings (McKinney M.S.). Preening was complete in loons on the second day (Beebe

1907), and oiling was functional on the third day. In terns (Van Iersel and Bol 1958) the movements were all present, but as in grebes there was little pressure to use them. Chicks up to five days never performed "more than 6 movements in succession (the average being 4.2), unlike the adults, which perform 100 movements or more." As in the grebes the tail and wings were neglected and most attention given to the breast, back, shoulder and wing bow. The authors state that these are low intensity preening movements. In Song Sparrows (Nice 1943) incomplete preening movements to the wing and breast occurred at five days before there were any feathers.

Adaptive correlates: A number of preen gland removal studies showed that feathers maintained their water resistance without oiling even after a molt. (See Fabricius 1957-58). Droplets of oil could be seen when feathers were dyed with Sudan III, even when the feathers used were from ducklings which had lost their waterproofing. Oil could not be taken from the preen glands of live birds but could easily be removed at death. In adult birds the secretion was in such small quantity that it would be seen only with difficulty. Fabricius (1957-58) removed the preen glands of hatchling tufted ducks before the birds dried, and preening movements continued normally. The operated birds remained completely waterproof, and there was no sign of oil on the feathers when they were examined microscopically.

Waterproofing improved with preening, and was lost if the birds were prevented from preening. It was lost from dragging the feathers in the pen, fouling with feces, such food as crushed fish or crustaceans, or from handling. Hooks on the barbules were poorly developed in downies. Feathers from waterproof birds were all in order, but in wet birds the barbules were in groups or across each other leaving gaps. From these experiments Fabricius concluded that the function of the oil and oiling was not primarily for waterproofness. He suggested that vitamin D might be involved, but this has since been disproved (See McKinney M.S.). The oil presumably helps maintain the structure

of the feathers and the condition of the bill and feet.

Young grebes are easily soaked at first and react to being put in the water by strenuously trying to get out. Some birds began to preen thoroughly after being put in the water from the fifth day. Others at four and five days still climbed directly into a warm spot and went to sleep. What waterproofness they had was restored as soon as the birds were dry. By seven days all the birds preened continuously after being in the water until they were thoroughly dry. The dorsal parts and wings were most easily wetted, and the birds tended to concentrate on these where drops had splashed or where the wings had been dragged in the water. Perhaps it is not possible for the young bird to preen while on the parent's back without disturbing the adult or falling off. Certainly while they are not waterproof, it is necessary for the young to remain on the parent's back. As preening and oiling develop together the birds gradually spend more time in the water. Whether oiling is necessary for waterproofness in grebes was not determined, but where the young were oiled very lightly by the observer, water resistance was improved. Heavier oiling of course destroyed water resistance completely.

Handling did not affect the waterproofness of grebes. They did not struggle and did not need to be confined. They could easily be lifted on an open hand, and the feathers were not disturbed. The ducklings were soiled from dragging their feathers on the pen floor, but this did not affect the young grebes. The belly feathers of the young grebes were finer and more closely interlocked than back feathers when seen under the microscope. They were also denser, and resisted wetting well as long as they were not soiled by feces.

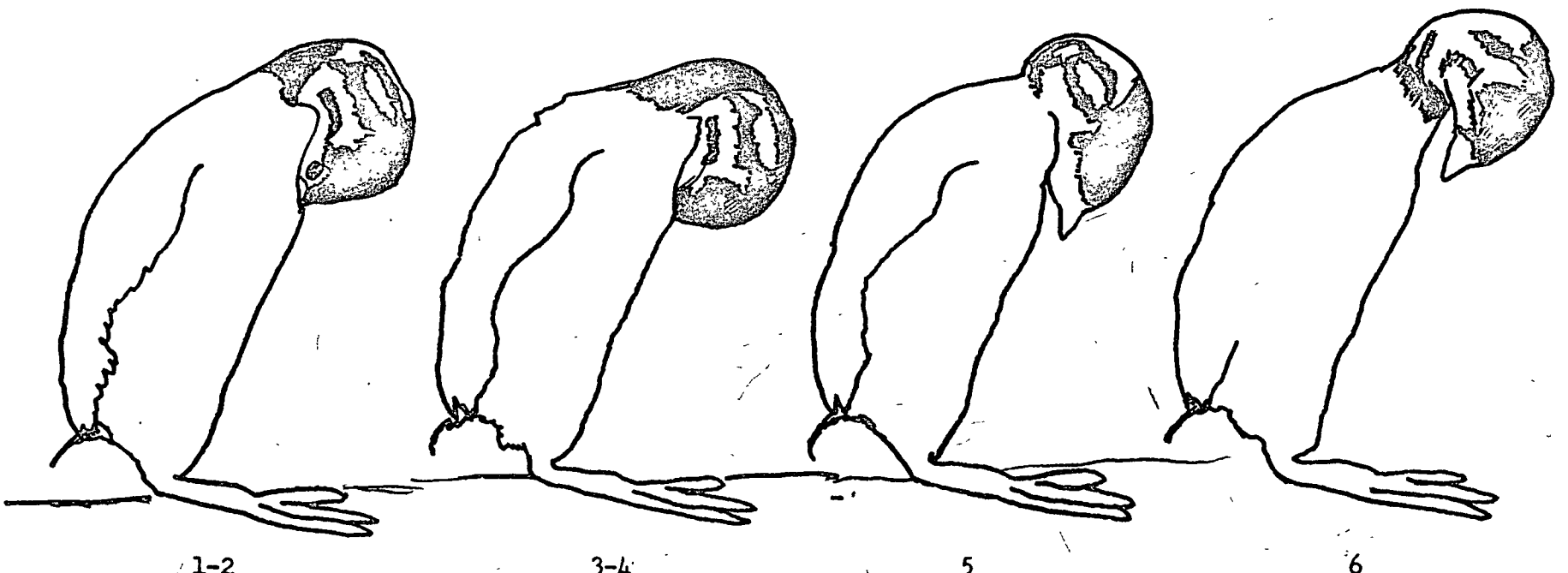

Fig. 24. Preening upper breast feathers.

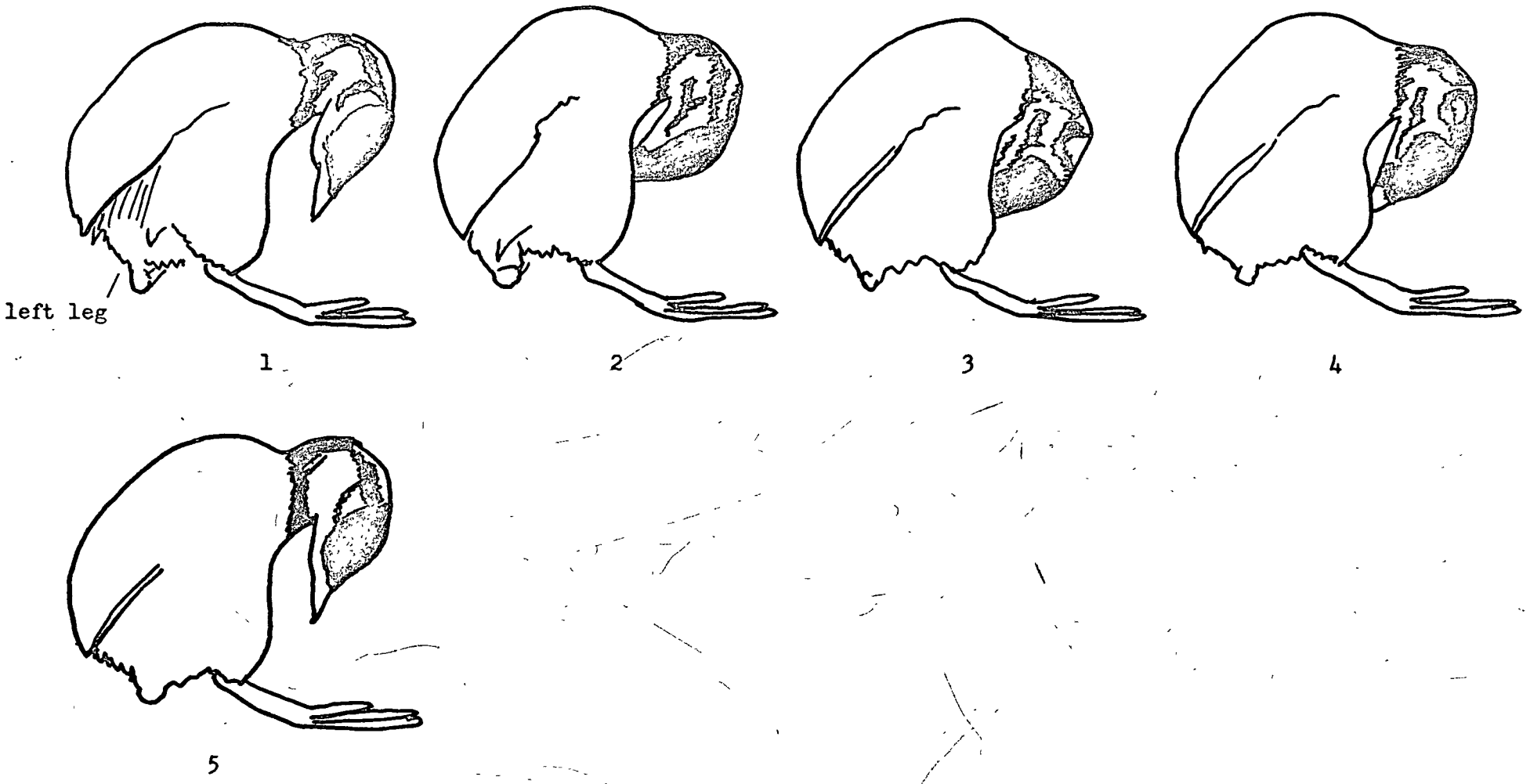

Fig. 25. Preening belly feathers.

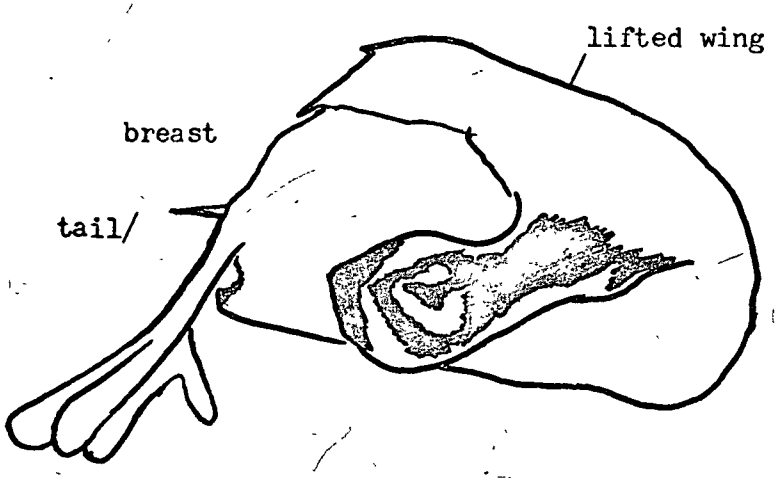

Fig. 26. Preening breast feathers lying down on platform, same posture as used in water.

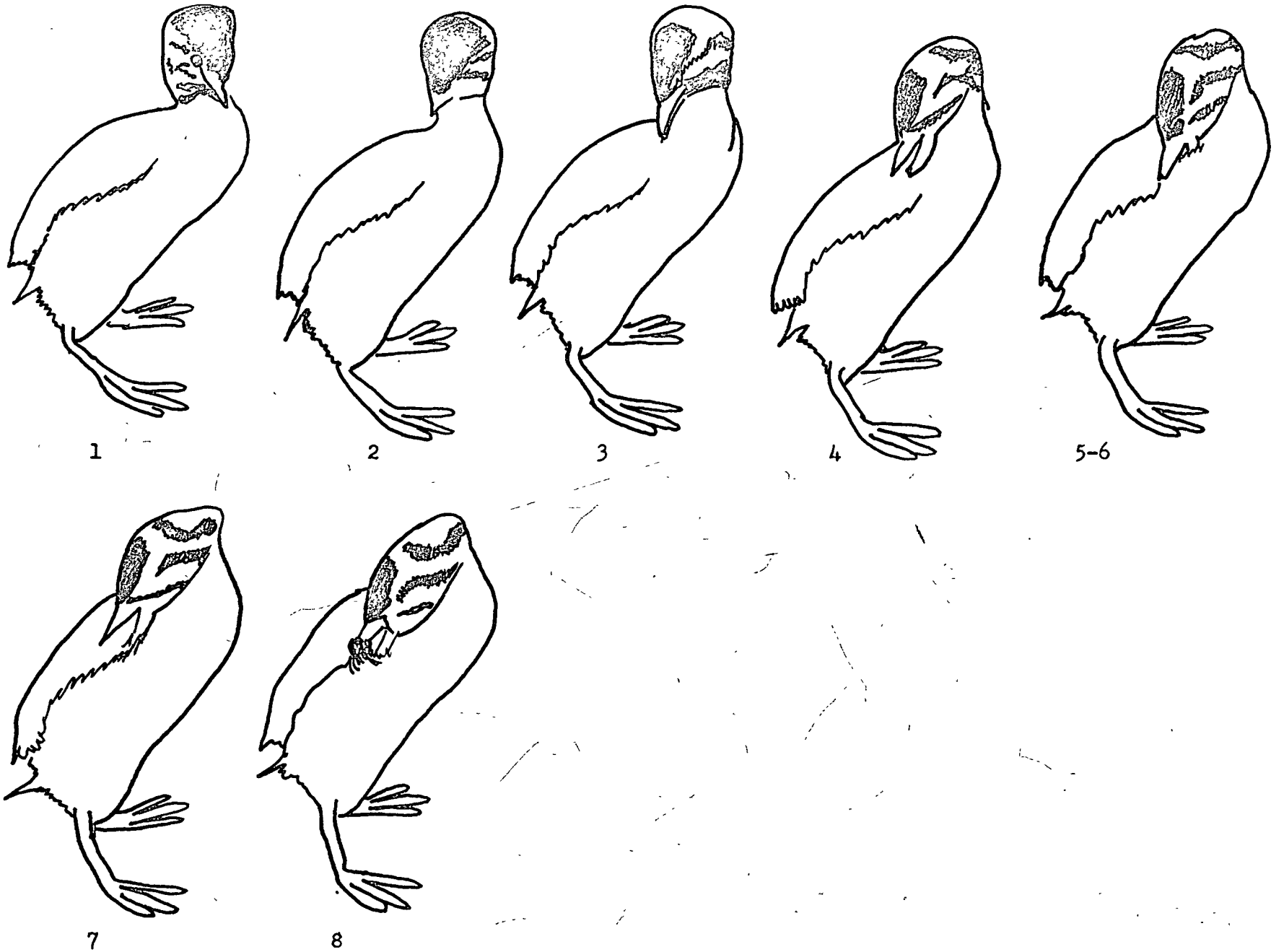

Fig. 27. Preening side feathers.

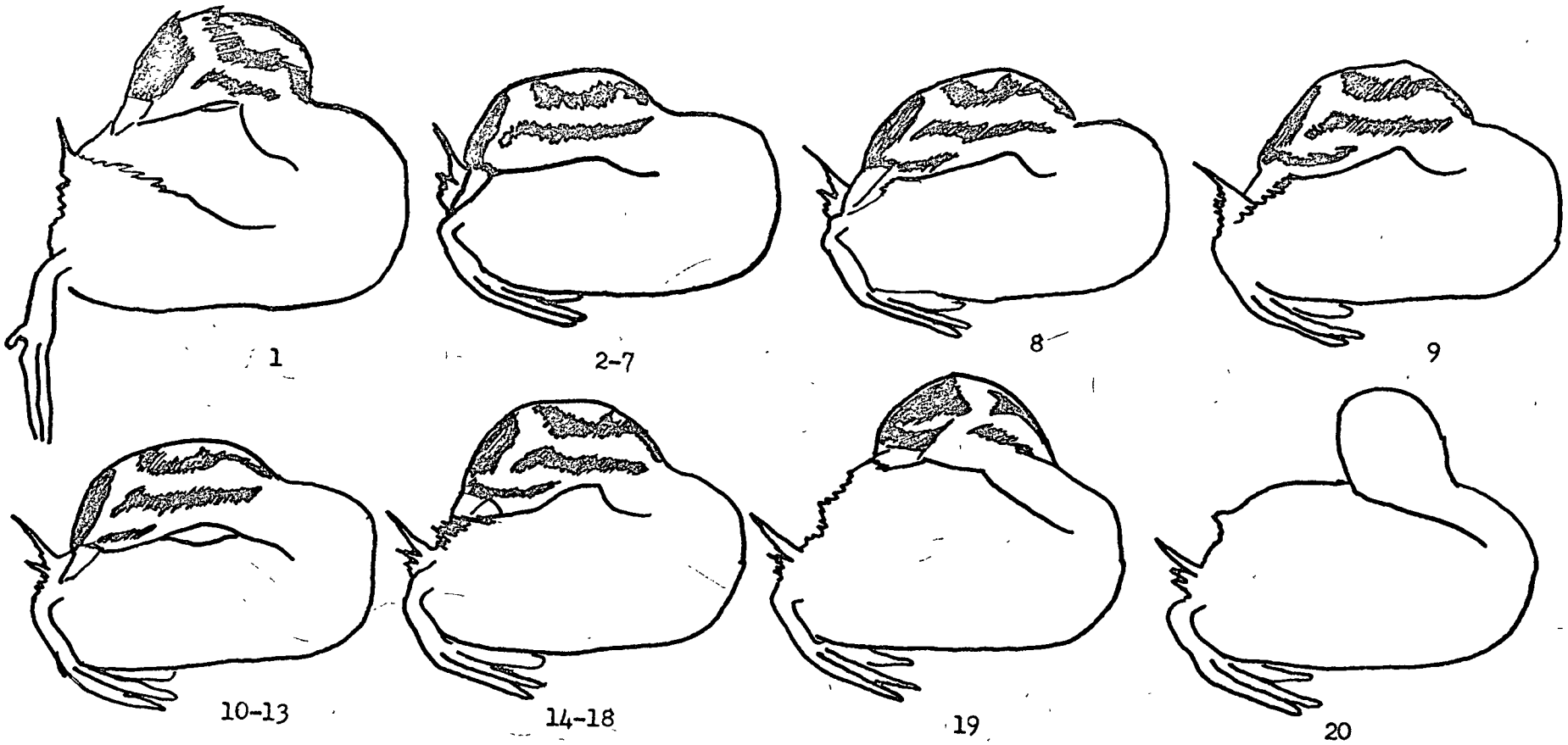

Fig. 28. Preening feathers right of tail.

Fig. 29. Preening secondaries.

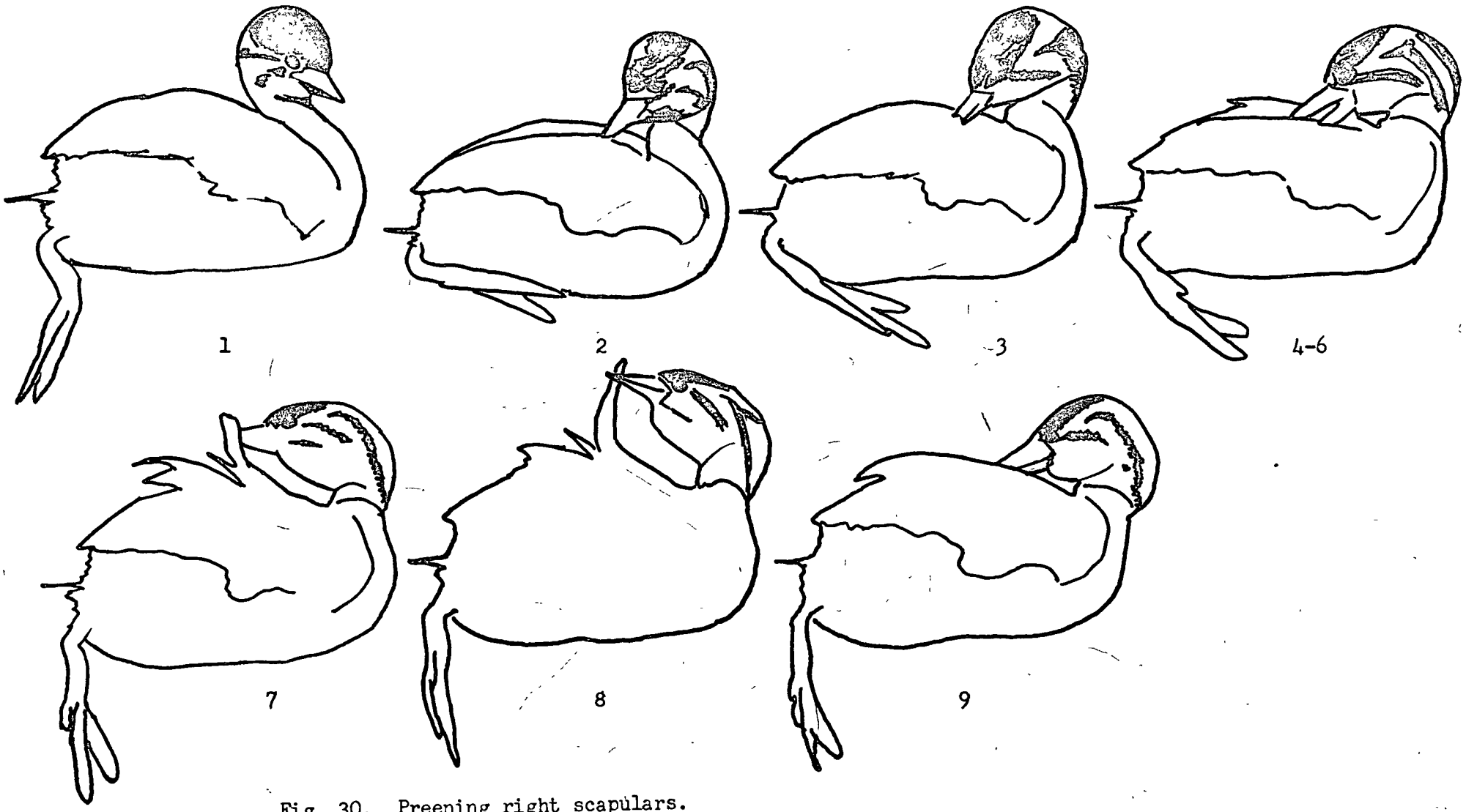

Fig. 30. Preening right scapulars.

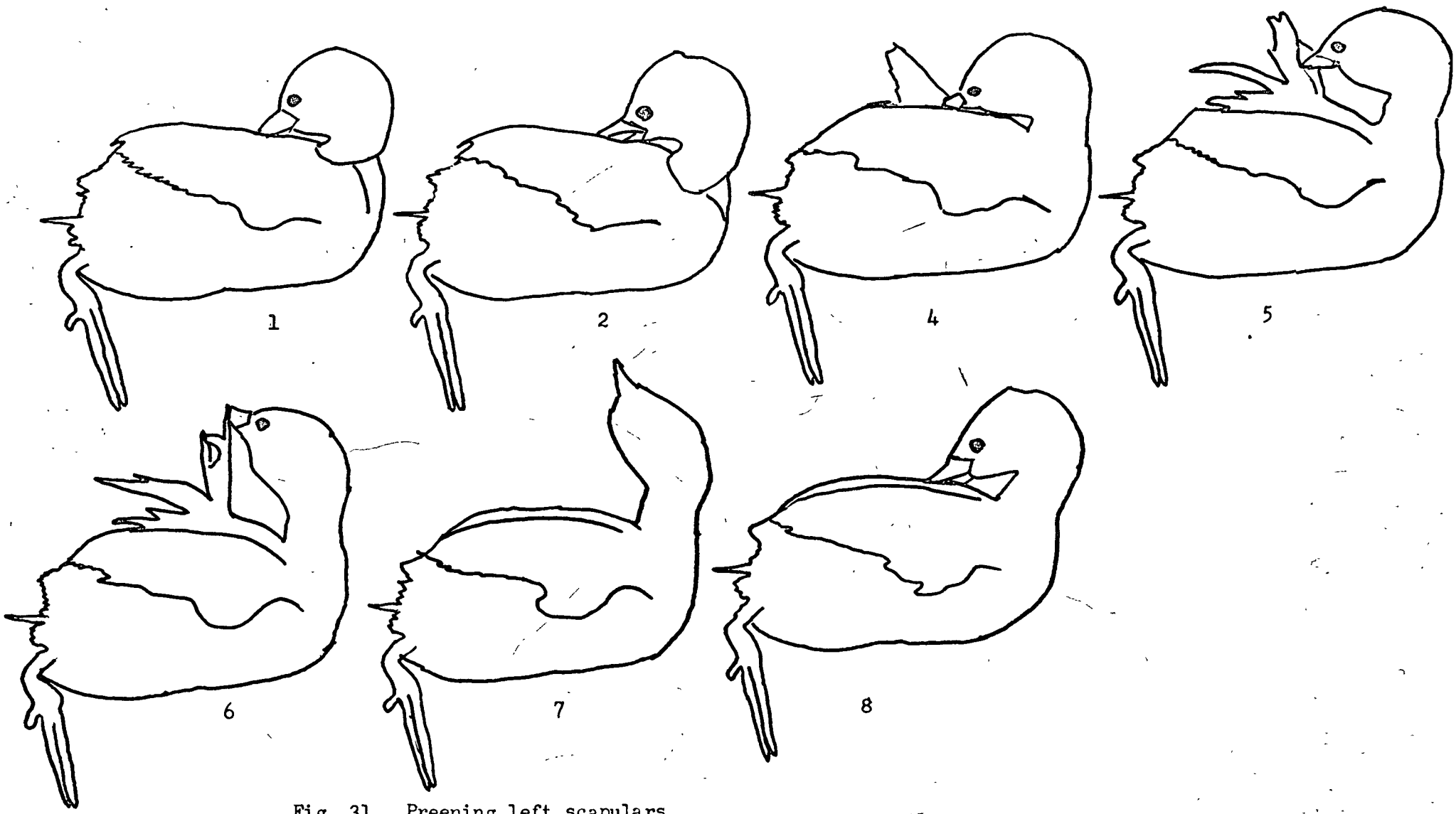

Fig. 31. Preening left scapulars.

Fig. 32. Nibbling preening under right wing.

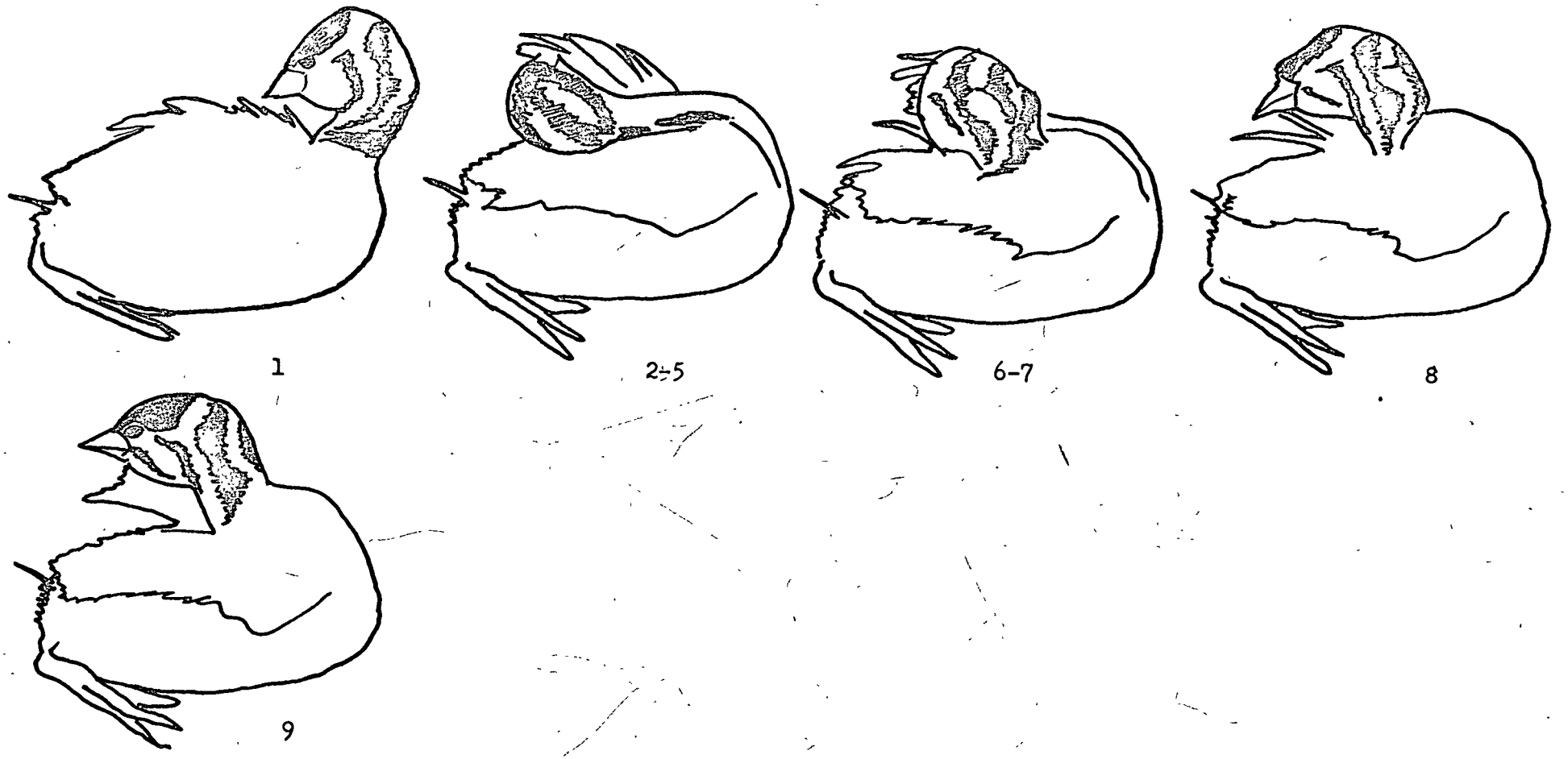

Fig. 33. Preening left wing coverts.

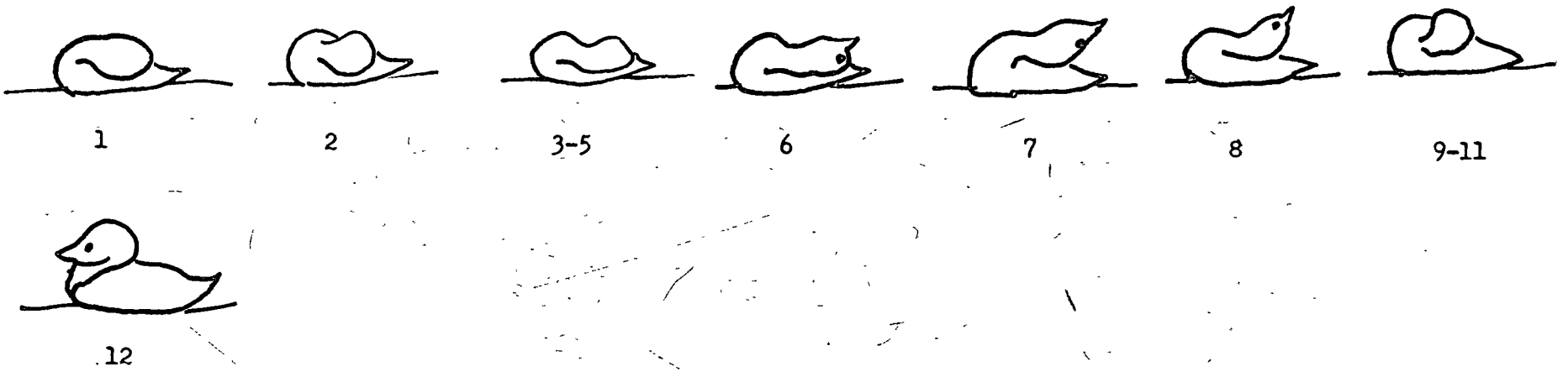

Fig. 34. Rubbing head on the oil gland.

PHYSICAL DEVELOPMENT

Feather Development

Problem: The first down is short and so thin that the skin can be seen without ruffling the feathers. When in the water more than a few minutes, the young bird becomes chilled, and as the down gets wet, the bird sinks lower and lower in the water. If it does not get out quickly, it drowns. It has the down plumage of a nestling, not that of a bird which must be independent on the water at least some of the time. Before it can spend much time in the water, the chick must develop a second thicker and waterproof down plumage.

Down is a perfectly satisfactory insulation in the water, although it is more easily wetted than contour feathers. But to become a flying bird it is necessary to assume a covering of contour feathers. The only birds maintaining a down-like covering into adulthood are those which do not fly. It does not matter in what order the feathers develop as long as there is no loss of waterproofing during the molt interval. Grebes do not get out of the water to dry and preen, and it is most important that the breast feathers be dry. Therefore the breast feathers are the first to develop. The next important area is the scapulars which cover the wings and keep the wings, back, and upper sides dry during diving. Then the less essential side, back, and head feathers develop, and finally the wings which are not needed until the fall migration.

Development: The following account is taken from a hand reared Pied-billed Grebe where the speed of development could be checked by observing wild siblings. It would not have been possible to see these subtle changes clearly in wild birds, even were it possible to know their exact ages. Correlations with behaviour are shown in Table XXV, the timing of the changes in Table XXIV. See also wild observations, Table II.

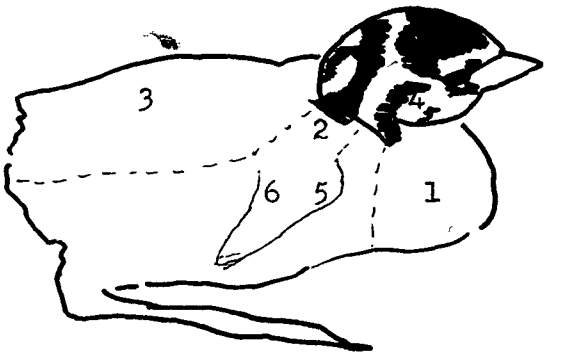

Table XXIV. Feather Development in One Pied-billed Grebe

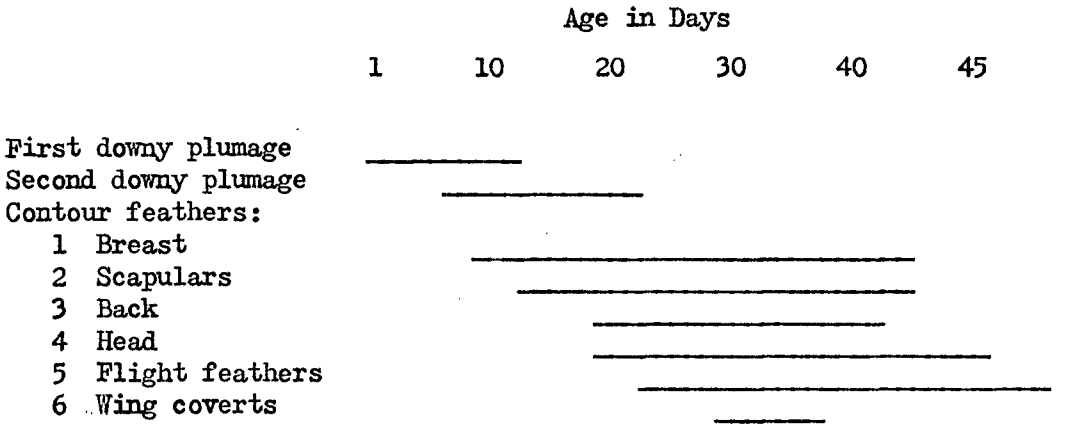

Table XXV. Correlation Between Physical Development and Behaviour

Physical Development		Behaviour	
Second down begins	7 days	Preening, oiling functional	6-7 days
		Scramble out of water to	7 days
		Swim voluntarily	8 days
Full second down plumage	10 days	First diving	10 days
Needed no heat source	10-12 days	Climbing diminishes	12 days
Breast well feathered	18 days	Diving frequently	16 days
Scapulars cover wings	18 days	No climbing	18 days
Wing functional	7 weeks	Flight	after 7 weeks

Second downy plumage: During the second week the original (protoptile) down feathers became damaged on the ends, and new (mesoptile) down feathers grew between the original ones. The new feathers were all grey and caused the velvety black and white of the original pattern to become more and more diffuse.

Further diffusion of the down pattern came as the original black and white down feathers themselves began to grow again. The new parts were grey with the black or white clinging to the end. Gradually the original feather material was broken off until on the eighteenth day only about a quarter of an inch of old white fluff was still attached to the grey down beneath. The black was finer and more fragile than the white and had completely disappeared a few days before.

Breast feathers: The first contour feathers appeared on the anterior breast (sternal portion of the ventral tract). The breast feather development had almost reached the anus before the scapulars began to appear. Each down feather was carried out on the tip of the contour feather developing in the same papilla. It remained in contact with the end of the contour feather until the contour feather was mature and fully spread. Then it was broken off by preening.

By the eighteenth day the breast feathers were well developed but still down-covered. The down wore away gradually, first from the front midline by the twenty-second day, about half way back (abdominal region of ventral tract) by twenty-four days. At this point the feathers were expanded to within an inch of the anus. When the anus was reached, the feathering advanced further up the sides, down covered until the thirty-fourth day, free of down by forty-three days.

Scapulars: The next feathers to develop were the scapulars (humeral tract). They grew to precisely cover the folded wings by eighteen days. The purpose of these feathers is to cover the folded wing giving a smooth waterproof surface during diving, and as the wing grew, the scapulars exactly kept pace.

Wings: The wings were down-covered during the first three weeks. They retained the first down, and no new feathers grew between the first. The down on the wings was longer than that on the body, but the wing appeared more and more naked as it increased in size. The primary and secondary sheaths showed through the skin on the twenty-second day, tipped with down as were the contour feathers. The quills of the flight feathers started to open at the end of the fourth week, and the sheaths of the coverts had appeared. The coverts, like the body feathers, opened almost as soon as they appeared, not with the long delay of the heavily sheathed flight feathers. The small feathers covering the leading edge of the wing (marginal coverts) had still not appeared by the end of the fifth week. By six weeks the wing was completely feathered, but the primaries and secondaries were still not completely unsheathed. By seven weeks when the bird was released, several of the primaries still had sheath material at the base. The wing was probably functional at this time, although the bird made no attempt to use it.

Back and head: The down on the back and head (capital and spinal tracts) became exceedingly thick, but there was no sign of the appearance of contour feathers until the end of the third week. At this time feather sheaths could not be felt but the down on the head suddenly appeared longer and fluffier. Feathers were apparent beneath the down on the head at three and a half weeks. As the down on the tips of these feathers began to break off, the white stripes on the head began to disappear. The first were the white eyebrow markings in the midline and front of the head. The abrasion needed to break off these down feathers came from scratching. By six weeks the head plumage (capital tract) was free of down to the posterior edge of the eyes. The cinnamon spot in the center of the head and the cinnamon band behind it had become very diffuse, and the white and cinnamon circle on the anterior dorsal surface of the neck was more diffuse than the head markings. Below this the dorsal neck feathers had been rubbed clear of down as they rested on the back and were glossy black. The sides and flanks (femoral tract) and the back (spinal tract) were also completely down-free by six weeks. The under tail coverts began to be conspicuous in the down by five weeks, and the whole tail was well developed by six weeks. The feathers of the head were down-free at six and a half weeks.

Egg-tooth: The bill of grebes is tipped at hatching with a relatively large chalk-white egg tooth. Most of the development was on the upper mandible, but a small flat plate also appeared on the tip of the lower mandible. See the photographs in Plate III. The tooth did not drop off, but gradually flattened and disappeared on the surface. Only a sliver of egg tooth material remained on the lower mandible on the fourth day, and

this was gone on the ninth day. The tooth on the upper mandible was thin on the sixth day. A thin plate remained on the eleventh day, and it was completely gone by the eighteenth day.

Soft parts: At hatching and until the end of the first week in Pied-billed, Eared, and Red-necked Grebes, the iris was black and the scales of the legs were black and glossy. At the end of the first week the feet appeared dry and were lightly oiled every day until this condition improved. By the end of the third week the iris was grey and speckled, but at what time this change occurred was unfortunately not noted. At this time the black scales on the legs were wearing off and the new larger ones were greenish. At five weeks the feet were blue with darker, almost black, portions along the bones. The feet of Western and Horned Grebes were pink-edged during the first 24 hours and then black with yellowish edges.

The bare skin spots on the heads of grebes are bright pink at hatching and for some time afterwards. In the Eared Grebe they become brighter when the chick is excited, particularly when it is hungry and begging. This with the striping of the head and the bright pink mouth serve as stimuli to the parent to feed the young. The patterns are strikingly species specific, presumably to ensure that the adults do not feed young of another species. The bare spots fade gradually during the first week, the ring around the eye fading faster than the head spot and the base of the bill. In the Pied-billed Grebe the eye ring was completely grey by the end of the fifth week, but the base of the bill was still bright pink. In the Horned Grebe the shields at the base of the bill were grey at six days, but the head spot was still bright pink.

Comparisons: Development of the loon seems to be similar. Loon chicks (Olson and Marshall 1952) have two downy plumages, the heaviest down occurring on the underparts. The second, lighter-coloured down replaces the

first during the second and third weeks, primarily through renewed growth of the down feathers, though there may be some fading. As in the grebes the first primaries begin to appear by the third week. The juvenal plumage is a little slower to be completed in the loon. It was rapidly replacing the down within five or six weeks, and the birds were in full juvenal plumage by from eight to ten weeks.

The order of development of contour feathers varies greatly from group to group, particularly the time of appearance of flight feathers. In the galliforms there is a great premium on the development of wings, and functional flight feathers are produced within six or seven days. Heinroth (1958) gives many other examples of precocial wing development. Waterbirds delay the development of wings in favour of waterproof body coverings. Ducks start with the scapulars and back, then wings and breast, and finally head and tail. As they spend some time on land, they do not need to develop the breast feathers first. Also in grebes (Heinroth 1928) the molt of the breast feathers is not a seasonal one; the feathers are being continually replaced. This means that they are always in the best possible condition and also provides an uninterrupted supply of feathers for the birds to swallow.

Chilling

During the first to fifth days the chicks spent all of their time at the warm end of their box, on an electric heating pad. By six days they chose the warmest spot for sleeping but were often in cooler areas when awake. They slept away from the heat source from about two and a half weeks.

Young grebes are extraordinarily susceptible to chilling. During the course of this study about forty chicks were lost as a result of cold. Draft was fatal even when the birds were huddled under an infra-red heater. Most deaths occurred when the bird were between 36 and 48 hours old, but they were possible during the whole first week, and a severe draft killed chicks up to twelve days. The birds refused to eat a few hours after being chilled, became listless and drowsy, and died in about twelve hours with laboured breathing and continuous soft cheeping. All were autopsied, and they showed congested and hemorrhaged lungs. No birds which died of other causes showed these symptoms. Beebe (1907) lost two loon chicks when the heat went off overnight. The birds were dead in the morning "and their lungs were extremely congested".

This susceptibility to chilling is the reason for continuous brooding during the first week. In this respect grebes seem to be much less precocial than the ducks and galliforms, and probably even than the gulls.

When allowed a choice of temperature between 80° and 100°F. in a box with a lamp at one end, a group of ten Western Grebes moved from one place in the box to another. When they settled in a heap to sleep the temperature at that point was taken. The temperature at any one spot in the box varied considerably from time to time. The choice of temperature was higher when the birds were wet than when they were dry. See Table XXVI. This shows the dependence of the birds on an external heat source at this time.

Table XXVI. Preferred Temperatures, Western Grebes 0-3 Days Old.

	No. Observations	Range Degrees F.	Mean
Dry birds:	15	80-96	87.0
Wet birds:	6	92-96	93.2

Weight

Problem: Sharp breaks in the weight curves of developing animals have been shown to correlate with changes in behaviour and physical development. To find these points of sudden change the weights of two captive Pied-billed Grebes were recorded. No weights are available in literature.

Methods: Measurements were made between 8:00 and 9:00 A.M. on a pan balance accurate to a tenth of a gram, and the birds remained motionless while the pans were balanced. At least half an hour had elapsed between the last feeding and weighing. Pellets were cast at irregular intervals after the twelfth day, but by this time the bird weighed over eighty grams. Since the pellets weighed less than two grams, most less than one gram, pellet weight did not affect body weight significantly.

Between the twenty-seventh and thirty-first days no local fish were caught, and fresh herring were cut into strips for food. The bird ate considerably less than usual making a sharp drop in the curve of weight. At other times the birds were eating to capacity. See Tables XXVII and XXVIII.

Table XXVII. Weights of Two Pied-billed Grebes.

	age days	wt. grams.	Second bird: age days	wt. grams
May 18	3	23.7		
21	6	35.0	1	12.5
22	7	37.5	2	13.9
24	9	53.4	4	23.7
28	13	92.2		
June 2	18	151.8		
3	19	164.5		
7	23	186		
8	24	198		
9	25	203		
10	26	211.6		

Discussion: There are three sharp breaks in the slope of the curve. One of these occurs between six and eight days, one between ten and twelve, and one at nineteen days.

At six days the birds were able to maintain the wings and feet on the back in the adult resting posture on land and in water, and they could hold their heads up longer. They were able to walk, preening and oiling were functional, and they were on the verge of beginning to spend some time on the water. The number of feathers eaten had suddenly increased. This corresponds to the age of leaving the nest in other precocial birds, the end of Mrs. Nice's developmental stage 3.

On the eleventh day the birds slept with their heads up in the adult resting posture. They had stopped flopping-forward and almost stopped climbing. Bathing had begun to be functional. The young grebes no longer needed an outside heat source at least during the day, and wild birds were brooded very little. The second down plumage was complete. This may correspond to the end of developmental stage 4 when more is found about the appearance of aggression.

At nineteen days the breast and scapular contour feathers were spreading though still down tipped, and feather shafts were appearing on the head and back. With this new feather covering, wetting and chilling were no longer a problem, and the birds were diving a great deal and picking up some food. They were nearly independent. This corresponds to the end of developmental stage 5, and the beginning of an independent juvenal period.

Comparison: Few studies are available on the growth of birds, and these present only arithmetic curves, usually mass curves showing the average growth of few to many birds. Lack and Silva (1949) on Robins and Vermeer (1963) on Glaucous-winged Gulls are two of these. All that can be said from these presentations is that the steep part of the curve occurs

between four days and four weeks in the gull and between two and eight days in the Robin. Brant (1951) found it possible to mathematically fit a single curve to the weights of individual chickens from one to twelve weeks. He considered growth to be smooth, without sharp changes. Changes in the growth rate were considered to be the result of atypical or diseased birds and discarded. He said that the growth rates of individuals must be considered in describing the growth of a species; a mass curve simply shows the extent of variability.

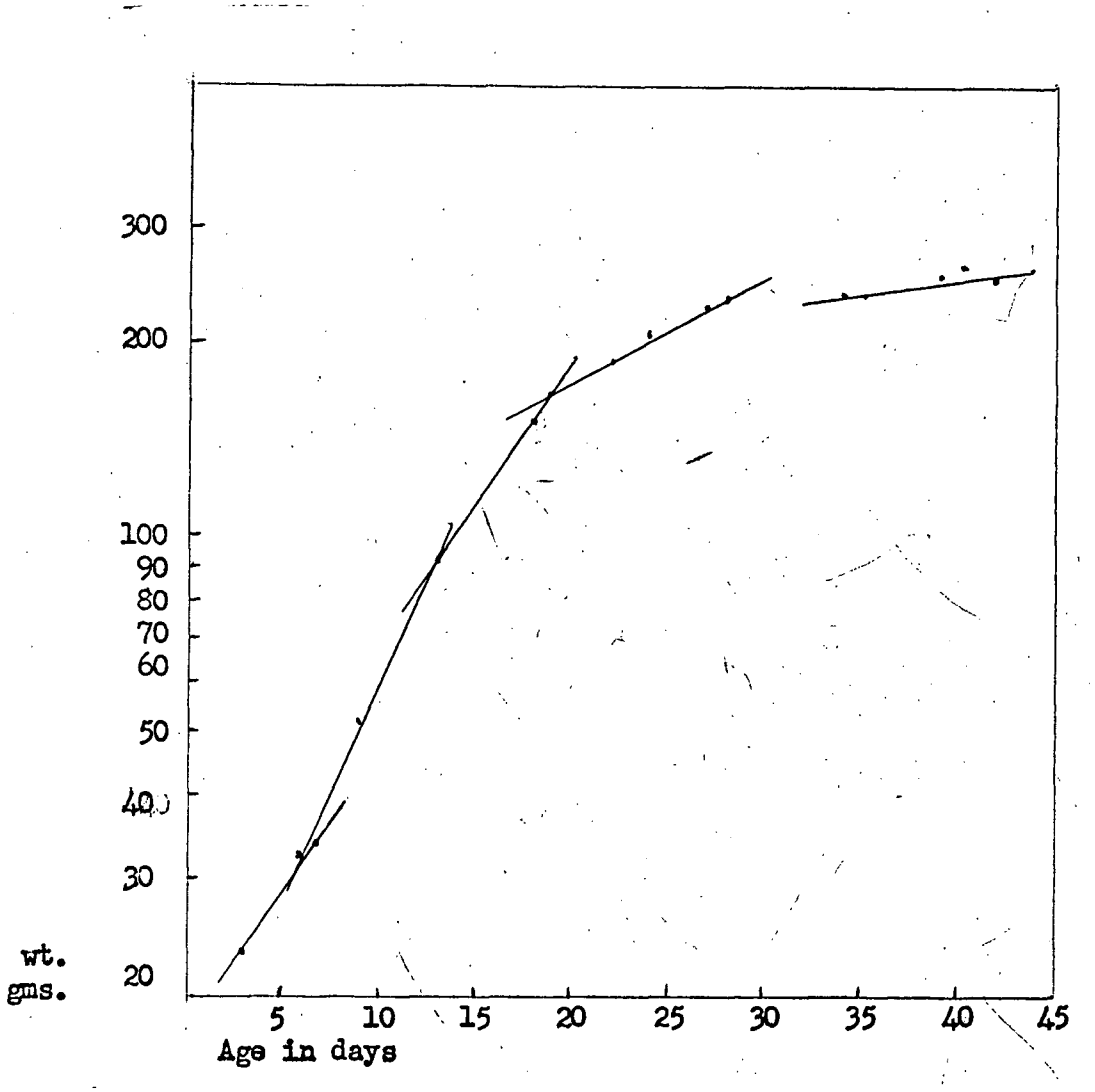

Table XXVIII. Weight of One Pied-billed Grebe.

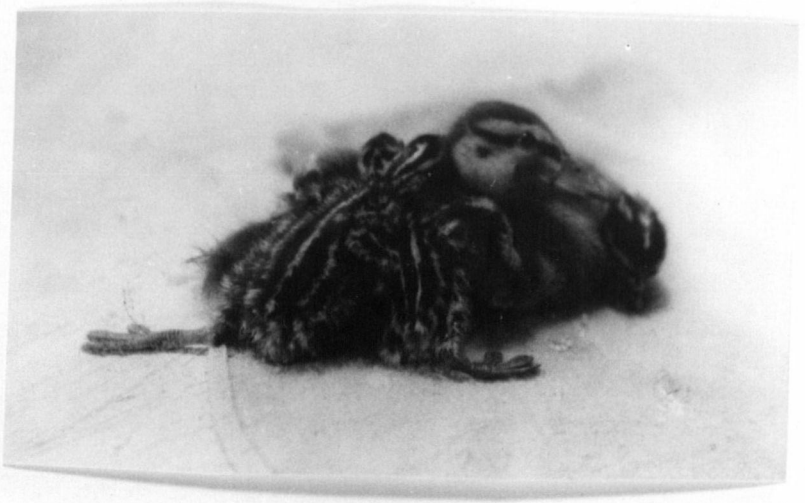

Plate V. Postures assumed by young grebes sleeping after climbing up on the back of Mallard duckling.

DISCUSSION

Placement of Grebes as Precocial Birds

Stages of development. The behaviour of precocial and altricial young has been divided into five stages (Nice 1962). The first stage of helplessness is passed in the egg in precocial birds. The second stage of first appearance of comfort movements takes only a few hours, and includes first appearance of stretching, standing, preening, and shaking. Stage three begins with the appearance of crouching and includes the maturation of comfort movements. It usually occupies the rest of the first day. Stage IV begins as the young bird leaves the nest, and includes self-feeding and fleeing. Stage V begins with the first use of aggression and includes socialization, and it ends with flight. The appearance of each behaviour pattern in grebes is shown in Table XXIX, XXX and XXXI. The patterns listed (Nice 1962) as occurring in the same stage in all groups are marked in column 3 of the table.

In grebes stage II lasts until the bird is dry and climbs onto the parent's back, one or two hours. The jaw-stretch and flopping-forward are nearly always seen, begging usually, and the comfort movements vary considerably from one individual to another.

Stage III begins in other groups with crouching, but since crouching is in grebes replaced by climbing-up, climbing-up has been used as a criterion for the beginning of this stage. In each group stage III included the development of stretching and shaking movements, standing on the feet and exploratory pecking. The number of comfort movements seen per day in stage three was very small, and there was considerable variation as to which were used. Most were available, their use depending on circumstances. The birds spent most of the time sleeping, and stretching and wing and foot lifting movements were seen while the bird was asleep. When awake their

most conspicuous movement was continuous climbing-up. See Table XXXII for typical records of stage III behaviour. Walking off the tarsi is in grebes delayed until 15 days by reason of the position of the legs, and walking on the tarsi has been substituted as a stage III character. Preening consisted of only one movement at a time on the first day, and this often was incomplete. The number of bouts and the number of movements per bout of preening gradually increased until they were first vigorous and functional after the fourth day when oiling was begun. Oiling reached functional proportions in the Pied-billed Grebe on the fifth day. Exploratory pecking was regularly seen from the fifth day. The most conspicuous characteristic of stage III in the grebes is its length. Those of all the precocial and semi-precocial groups discussed in Nice (1962) ended at one day (Killdeer 2 days), while in the grebes it lasts until the eighth day.

Stage IV begins in all groups with leaving the nest, or where that information was not available, being "strong on feet". Although grebes were able to climb-up and flop-forward from shortly after hatching, they could not be said to be strong on their feet until they could move around at least on the tarsi, and began to maintain the resting posture of the adult in sleep and in swimming. In other groups the resting posture of the adult appears at the same time as leaving the nest, and the head in the Pied-billed Grebe is held up in sleep on the seventh day. Since there is no real nest-leaving (the chick spends almost all its time on the parent's back from the time it is dry and there is no change in behaviour associated with leaving the nest), spontaneous swimming has been used as the criterion for the beginning of stage IV. The chicks leave the protection of the adult's back and swim on their own voluntarily for the first time at eight days.

Table XXVIV. First Appearance of Behaviour Patterns, Pied-billed Grebe.

		Stage seen in all other groups:
Stage II		
Hatching to 2 hours.	Jaw-stretch	II
	Stand	II (on tarsi)
	Begging	
	Incomplete preen	II
	Drinking	
	Flopping-forward	
	Foot shake	
Stage III		
2-18 hours	Climbing-up	III (crouching)
	Wing-shuffle	III
	Feeding	
	Feather-eating	
	Wing-leg-stretch	III
	2-wing-2-leg-stretch	
	Head-shake	
	Swimming if necessary	
	Head-rubbing	
	Incomplete belly preen	
	Foot lift to resting posture	
	Wing lift to resting posture	
	Incomplete scratching	II
2nd day	Defecate standing	
	Rudimentary body-shake	III
	Scratching	
3rd day	First steps	III
4th day	Resting wings on back	
	Body-shake	III
	First oiling	
	Functional preening	
	Wing-flap standing	
5th day	Sleep feet up	
	Exploratory pecking	III
	Wings on back in swimming	
	Walk on tarsi	III
7th day	Head up in sleep beginning	
	Functional oiling	
Stage IV		
8th day	Second down begins	
	First pellet	
	Spontaneous swimming	IV (leave nest)
	Incomplete bathing	IV

10th day	Diving Wing-flap standing Following	IV
14th day	Head up in sleep Bill tucked in sleep	
15th day	Walking off tarsi	
Stage V		
16th day	Aggression	V
17th day	Matured bathing Alarm posture Second down complete	V
after 7 weeks	Flight	V

Stage IV in other groups also includes fleeing, picking up food, and simple bathing. In grebes the first incomplete head-dipping bathing movements appear with voluntary swimming at eight days, and diving with picking up food at ten days. Fleeing then takes the form of diving away as in the adult rather than climbing-up.

Aggression has been taken as a criterion for the beginning of stage V in all groups. Aggression was not seen in the grebes in the present study, but Nice (1962) reported it in a captive Eared Grebe at 16 days, and this is here taken as the beginning of stage V. Matured bathing and flight appeared in this stage in all groups. In the grebes matured bathing appeared on the seventeenth day, but flight was much delayed, to after seven weeks. The beginning of stage V is in ducks 11 days (McKinney M.S.), Killdeer 9 days, Spotted Sandpiper and chickens 7 days, Sora 14 days, Coot 5 days, and Franklin's Gulls 5 days (Nice 1962). The grebes fit at the end of this range, and it may be that further work will show that the beginning of stage V should be earlier. A more logical break in behaviour occurs after the 10th day.

Placement of grebes. The grebes have been placed (Nice 1962) in the group precocial 4, birds which are led by the parents and fed by them. But the grebe chick is not led by the parent in the first week; it is brooded constantly. It cannot stand cold, and its resting and sleep postures are not well enough developed for it to rest on the water. It does not voluntarily follow the parent, but overtakes and climbs on it. The eggs of grebes are small in proportion to the size of the bird, and the yolks vary from 22% in the large species to 29-31% in the Little Grebe (Heinroth 1928). This is within the range of both precocial 4 and semiprecocial groups. (See the Table 4, Nice 1962).

It is clear from comparison that the grebes do not belong in the group with the rails. They would be better placed after the gulls as semi-precocial birds, birds which do not leave the nest although they are physically able to do so. They are between the gulls and the semi-altricial birds. Their thin wettable down, inability to hold the wings and head up in resting on land and water, lack of functional preening, extended stage III with depressed level of activity, and lack of fear behaviour show them to be nestlings in structure and behaviour. They have in addition an external stimulus for defecation similar to that in altricial birds, and backing to defecate as in the gulls.

Adaptation

Cullen (1957) in a study of reproductive behaviour of the Kittiwake has given a very striking picture of the degree to which behaviour can be adapted to the environment. The basic behaviour patterns of gulls nesting on sandy beaches were well known, and almost every pattern was changed in

Table XXX. Development of Behaviour in One Horned Grebe.

		Stage seen in all other groups:
Stage II		
Hatching to 1 hour.	Preen 20m	II
	Shoulder-rubbing -22m	
	Jaw-stretch 27m	II
	Foot-shake 28m	
	Foot-lift 28m	
	Wing-lift 29m	
	1-leg-stretch 33m	
Stage III		
1 hour to 24 hours	1-wing-1-leg-stretch 1h	III
	Wing-flap, incomplete 1h55m	
	2-wing-2-leg-stretch 5h	
	Scratch, incomplete	
	Stand on tarsi 5h13m	II
	Body-shake 5h13m	III
	Scratch complete 20h	
5th day	Back to defecate	
	Wings up in swimming	
6th day	Preening functional	
7th day	Oiling	

Table XXXI. Development of Behaviour in Western Grebes.

Stage II		
from hatching	Climbing	
	Flopping-forward	
	Jaw-stretch	
	Head-flick 10m	
	Head-shake 15m	
	Bite and Swallow 25m	II
1 to 18 hours	Preen 3h -18h 6h	II
	1-leg-stretch -9h 14.5h 14h 4h	
Stage III	2-wing-2-leg-stretch 18h (only time seen)	
	1-wing-1-leg-stretch -3½d 2½d 27h 3½h 3¼d	III
	Shoulder-rubbing 2½d (only time seen)	
	Begging high intensity 3¼d 3¼d	II
	Body-shake 2d 4½d 5d	III
	Wing-flap 6d	
	Preening functional 5d 7d	
	Preen tail 7d	
	Oil 6d 8d	

the Kittiwake to suit it for nesting on narrow cliffs. This subtle coordination with all the factors of the environment is to be expected in every group by virtue of long evolution.

The grebes are adapted exclusively to a water habitat with their legs placed so far back that they walk with difficulty. They do not then come out on land even to nest, but build their nests of material which they obtain by diving. They can jump out of the water onto these low nests and escape easily by their only escape mechanism, diving. The nests in consequence are wet, easily swamped by waves, and subject to destruction by storms. It is an advantage to get the young away from them as soon as possible. The eggs are small and the incubation period relatively short. But because of this the chicks hatch in a relatively undeveloped state, with down so thin and short that the skin shows, and is easily wetted. They are easily chilled and drown if they become wet, and they cannot maintain the adult sleeping posture. They cannot stay on the nest, nor can they follow the parents in the water.

The adults do not fly to get food, so it is possible to take the young on foraging expeditions. The grebes carry their young with them, and become floating nests for brooding the young. The young are then really nestlings.

While the young are on the parent's back there is no pressure for fast development through stage III, and there is an advantage in having the chicks as quiet as possible. All activity is depressed, and stage III is extended to the end of the first week. While on the parent's back, the chicks cannot get food for themselves, and begging is well developed. They must not defecate on the parent's back, and the parents drop them off at frequent intervals into the water. The ordinary response of

defecation during a burst of strenuous activity ensures that the young defecate before they climb up again. If the parents do not drop the chicks off, the appetitive behaviour of backing before defecation will get the chick off the parent's back. Swimming, overtaking, and climbing behaviour are well developed so that the chicks can get onto the parent's back.

When the second down plumage has developed sufficiently, and the preening and oiling movements for maintaining the feathers have appeared, the birds begin to spend some time on the water. Following replaces climbing-up gradually, and diving, bathing, and self-feeding begin.

Table XXXII. Typical One-hour Stretches of Behaviour.

jaw-stretch	1-wing-1-leg-stretch	2-wing-2-leg-stretch	2-wing-stretch	head-shake	wing-flap	foot-lift to back	wing-lift to back	preen wing bow	preen side	shoulder rub	scratch chin	sleep	
													Pied-billed Grebe 18 hours
						2						|	8:30 A.M.
						12						|	
						8						|	8:40
						2						|	
						6						|	8:50
						6				1		|	
						3					2	|	9:00
												|	9:10
						1				3		|	
						9						|	9:20
						14						|	
1			1				3					|	9:30
1	1					3			1			|	
2					10								
													Red-necked Grebe $2\frac{1}{2}$ days
												|	7:30
3						3						|	
1						1						|	7:40
												:	7:50
1												:	
	3							2	3			:	8:00
									24			:	
1						1						:	8:10
1												:	
1							1					:	8:20
												:	
													8:30

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