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**Feather eating in Great Crested Grebes *Podiceps cristatus*:  
a unique solution to the problems of debris and  
gastric parasites in fish-eating birds**

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The occurrence of feathers in stomachs of 407 Great Crested Grebes *Podiceps cristatus* from Lake IJsselmeer, The Netherlands, is described. Only four of the 8718 identified stomach feathers originated from a species other than Great Crested Grebes. In all, 68% were breast and belly feathers and 19% were flank feathers. Flank feathers were positively selected from those becoming available during moult, and also occurred more in the ejected feather pellets than expected from the intake. This suggests that flank feathers, which are long and curved and have a black tip, may be especially suited for the formation of pellets. Feather ingestion was more than balanced by feather production. Feathers were most abundant in stomachs in autumn and were least numerous in winter. Most of this variation can be explained by seasonal differences in the intensity of body moult. In addition, the type of prey was related to the number of ingested feathers. When the diet consisted of smelt, which leave little indigestible matter, more feathers were eaten than with a diet of perch and pikeperch, which leave more fish debris. We suggest the hypothesis that ingested feathers, in the absence of other indigestible matter, contribute substance to the stomach content, enabling the formation of pellets that can be ejected. The habit of regularly ejecting the stomach contents minimizes the chance that any serious population of gastric parasites will build up in the upper part of the alimentary tract.

Grebes, Podicipediformes, eat large quantities of their own feathers (Buffon 1781, Madon 1926) and with this habit they are unique among birds (Fjeldså 1977, Simmons 1985). Parent grebes start feeding their own feathers to the chicks soon after hatching (e.g. Rankin 1947, Hanzák 1952, Simmons 1955, Vlug 1983). Intact feathers are not actively pulled out of the plumage, but only ingested after they are shed during moult. Many feathers are eaten during preening sessions.

Several hypotheses have been put forward to account for the feather eating habit in causal or functional terms (Buffon 1781, Madon 1926, 1931, Harrison & Hollom 1932, Hanzák 1952, Simmons 1955, 1956, Geiger 1957, Madsen 1957, Storer 1961, 1969). The general opinion is that ingested feathers are necessary for the formation and casting of pellets, in order to remove most of the stomach contents periodically. This paper examines the occurrence of feathers in the stomach contents of a large sample of Great Crested Grebes *Podiceps cristatus*, and suggests a new functional explanation for pellet casting.

### Materials and methods

In this study 407 Great Crested Grebe casualties from Lake IJsselmeer, The Netherlands, were examined for body moult and stomach content. The grebes were collected in the non-breeding seasons between

August 1978 and December 1985 after having drowned accidentally in gill nets. Within 36 h the birds were put in deep-freeze, at temperatures of  $-15$  to  $-20^{\circ}\text{C}$ . After thawing, the grebes were dissected and sexed by gonadal examination. Juveniles (first-year birds) and adults were identified by head pattern (Cramp & Simmons 1977) and the presence (in juveniles) or absence of brown lesser upper wing coverts (Piersma 1988c). Different parts of the inside of the skin (the feather tracts: head, neck, breast, belly, flank, back and scapulars) were examined for moulting feathers, which show up as protruding follicles (see Piersma 1988a for details). The abundance of follicles was scored as no (0%), light (5%), moderate (15%) or heavy (30% of the feathers in) moult. The moult of wing coverts was examined from the outside.

Five grebes (two males and three females) were plucked, the plumage dried and the different feather tracts weighed separately. The numbers of feathers on different tracts were determined for an adult female (data in Piersma 1988a), the number of small contour feathers being extrapolated by counting weighed samples. The total number (14,000) was the same as recorded in a juvenile male. The availability for ingestion of feathers of a specific feather tract ( $A_i$ ; in %) was calculated as moult intensity ( $MI_i$ ; in % of feathers) times the number of feathers on that tract ( $n_i$ ) divided by the sum of moult intensity times numbers of feathers of all feather tracts, thus:

$$A_i = [(MI_i \times n_i) / \sum_{t=1}^7 (MI_t \times n_t)] \times 100\%$$

The underlying assumption is that measured moult intensity (in % of feathers) accurately reflects the instantaneous feather production rates (cf. Piersma 1988a). Daily contour feather production rates were calculated from moult intensity (in %), feather mass and inferred feather growth rates, as outlined by Piersma (1988a).

For each grebe the stomach, including the proventriculus, was removed from the carcass and opened. The stomach contents (a feather ball with fish debris) were stored in 96% ethanol. Care was taken to also collect the small group (two to six) of feathers which was always present in the small extension of the stomach cavity near the pylorus (the opening to the intestines). Feather balls were of variable size and colour, from light greyish green in the large (fist-size) balls, to a very dark green in the small (thumb-size) ones. Their size depended on the quantity of undigested fish meat and the number of feathers.

To analyse the stomach contents, a feather ball was put in a 2-litre measuring glass, and the light feathers floated off from the heavier fish and plant fragments by a water flow. The fish fragments consisted of vertebrae, scales, otoliths, parts of jaws and pharyngeal bones, which were all easily identifiable. The lengths of right pharyngeal bones (in the cyprinids bream *Abramis brama* and roach *Rutilus rutilus*) or the otoliths (in the salmonid smelt *Osmerus eperlanus* and the percids ruffe *Gymnocephalus cernua*, perch *Perca fluviatilis* and pikeperch *Stizostedion lucioperca*) were measured to the nearest 0.1 mm with a micrometer mounted on a binocular microscope. The total number of right side otoliths or pharyngeal bones was assumed to reflect accurately the total number of fish in the stomach. Fresh mass was exponentially related to both pharyngeal bone and otolith length. The predictive equations used in this paper to estimate ingested fish mass are presented by Piersma (1988b).

The feathers in the stomach were dried and weighed to the nearest 0.1 mg. Feather samples of 104 individual grebes were sorted. A reference collection was made and the feathers identified as belonging to the following feather tracts: head, neck, breast and belly (not separately identifiable), flanks, back, scapulars and wing coverts; or were identified as of non-grebe origin. The sorted and identified feathers were counted, put together, dried again and weighed. It thus appeared that the gross feather mass consisted of 63.7% (s.d. = 12.4%,  $n = 90$ ) intact feathers, the rest being small parts of partly digested feathers, and dried plant and mucous material. All stomach feather mass values presented here refer to net mass, resulting from either weighing samples of sorted feathers or from multiplying gross feather mass by 0.637.

Computations were performed with a standard statistical package (SPSS, Nie *et al.* 1975). In a multivariate analysis, stomach feather mass and ingested fish masses were log-transformed to obtain normal distributions. The standardized residuals were plotted to check whether normality was achieved. Non-parametric tests are according to Siegel (1956).

## Results

### Mass, numbers and types of ingested feathers

Great Crested Grebes have about 14,000 contour feathers which together weigh almost 36 g. The feathers of the head are smallest and weigh 0.4 mg each, whereas

Table 1. Mass and numbers of feathers found in stomachs of Great Crested Grebes in the course of the non-breeding season. Note that the sample sizes for feather mass values are much larger than those for feather numbers

Month	Stomach feather mass (g)			Total numbers of feathers		
	Mean	s.d.	n	Mean	s.d.	n
July	0.308	—	1	48	—	1
August	0.482	0.236	30	118	54	28
September	0.458	0.338	38	121	99	27
October	0.306	0.224	37	90	40	14
November	0.262	0.229	71	27	21	21
December	0.140	0.154	55	12	6	3
January	0.126	0.076	17	20	—	1
February	0.065	0.070	104	21	27	6
March	0.136	0.140	54	26	12	3
Mean	0.211	0.234	407	83	73	104

scapulars weigh as much as 12.6 mg (Piersma 1988a). On average, a grebe stomach contained 83 individual feathers which together weighed 0.211 g (Table 1). No differences could be found between males and females, or between juveniles and adults of either sex. The average mass and number of stomach feathers varied over the season, feathers being most numerous in autumn. In midwinter stomach feathers were not particularly abundant. The number and mass of feathers in the stomach were linearly related [dry mass (g) = (0.0038 × n) + 0.043,  $r^2 = 0.92$ ,  $n = 104$ ]. Again, no differences were detected in the regressions between males and females, or between juveniles and adults.

### The selection of feather types

Hanzák (1952) and Simmons (1956) noted that Great Crested Grebes mainly take the small white feathers of breast and belly. Our data (Table 2) confirm this pattern: 68% of the 8718 identified stomach feathers originated from the breast and belly feather tracts. This percentage is larger than would be predicted if feathers were taken according to their abundance on the body and assuming equal overall production/moult rates between feather tracts (the latter is not entirely true, see Piersma 1988a). Flank feathers also occurred in larger numbers than expected, whereas head and neck feathers, scapulars and wing coverts occurred less (Table 2). Four diving duck *Aythya* spp. flank feathers were found, which shows that grebes sometimes ingest feathers that are not their own.

In order to correct for differences in moult intensities among feather tracts, data were selected for individual grebes for which both body moult intensity and stomach feather content were known. Plotting the relative availability of a specific feather type ( $A_i$ ) against the relative presence of that feather type in the stomach content, it was possible to see whether or not this feather type was selectively ingested by a grebe (Fig. 1). Since a grebe may be unable to pick off loose feathers from its own head and neck, we have calculated different overall availabilities, either or not including the (moulted) feathers of head and/or neck. Under all conditions flank feathers occurred significantly more often in the stomach content than expected from

Table 2. Feather types found in 104 stomachs of Great Crested Grebes, in relation to the relative abundance of the feather types on the grebes. The null-hypothesis, that the two percentage distributions do not differ, was rejected at the 0.1% level ( $\chi^2 = 88.0$ ,  $P < 0.001$ )

Feather type	Feathers in the stomach		Percentage of contour feathers
	Total number	Percentage	
Head	107	1.2	15.8
Neck	246	2.8	25.9
Breast and belly	5929	68.0	35.9
Flank	1682	19.3	7.2
Back	515	5.9	5.7
Scapulars	77	0.9	2.0
Wing coverts	158	1.8	7.5
Diving duck feathers	4	0.1	—
Total	8718	100	100

their relative availability (Table 3). Breast and belly feathers were ingested more than expected under two conditions, but not statistically significantly so when both head and neck feathers were considered entirely unavailable.

We conclude that flank feathers are positively selected and ingested from the assembly of feathers that are lost during moult. Breast and belly feathers may also be positively selected. The finding that some feather types are selected over others implies that only some of the moulted feathers are actually ingested, the proportional 'losses' being least for flank, breast and belly feathers.

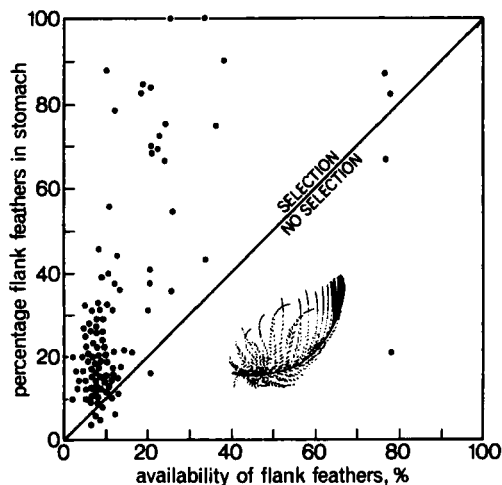


Figure 1. The ingestion of flank feathers by Great Crested Grebes in relation to their availability as shed (moulting) body feathers (for calculation of feather availability see text). Points represent individual grebes collected throughout the non-breeding season.

Table 3. *Statistics to examine whether flank or breast-and-belly feathers are ingested selectively by Great Crested Grebes (n = 104). The null-hypothesis is that the number of grebes selecting a feather type (above the diagonal in Fig. 2) is equal to the number that does not or selects against that feather type*

Feather type (FT)	Source of ingested feathers	n with selection for FT	n without selection for FT	Sign test	
				z-score	one-tailed significance
Flank	All contour feathers	94	10	-8.14	$P < 0.0001$
Flank	All, minus head feathers	89	15	-7.16	$P < 0.0001$
Flank	All, minus head & neck feathers	72	32	-3.82	$P < 0.001$
Breast & belly	All contour feathers	86	18	-6.57	$P < 0.0001$
Breast & belly	All, minus head feathers	84	20	-6.17	$P < 0.0001$
Breast & belly	All, minus head & neck feathers	46	58	1.08	$P = 0.14$

### Correlates of ingested feather mass

Numbers of feathers in stomachs were largest in autumn and smallest in midwinter (Table 1), periods when Great Crested Grebes show very heavy and light body moult intensities, respectively (Piersma 1988a). This suggests that the abundance of ingested feathers may be partly explained by the number of feathers on offer (the individual's moult intensity). Figure 2 confirms this possibility, showing that stomach feather mass is positively correlated with contour feather production rate, no differences in the regressions for juveniles and adults being apparent. The huge spread in stomach feather mass values is not unexpected, since some grebes should just have ejected their stomach content when captured, whereas others should be about to do so. The fact that few stomach feather mass values were larger than twice the daily contour feather production rate, supports the observations (Kop 1972, pers. obs.) that 'feather pellets' are produced every other day. In the wild, pellet casting is only rarely observed, but appears to occur especially before feeding episodes (Storer 1961, 1969, O'Donnell 1982). When monthly average masses of stomach feathers (Table 1) are plotted relative to monthly average feather production rates (Fig. 2), it appears that they closely follow the regression line calculated for the individual data points.

Although variations in body moult intensities explain much of the variation in stomach feather masses, we had the impression that stomachs with many otoliths of smelt contained more feathers than stomachs containing mostly the remains of other fish. In the sample of all grebes collected in the non-breeding season, those that fed predominantly on smelt indeed contained more feathers than those that did not (Fig. 3 left). However, during autumn (many feathers available) smelt contributes more to the diet of Great Crested Grebes than during winter (few feathers available), and this alone might explain the pattern. When the analysis was repeated separately for two bi-monthly periods for which large samples were available, the trend for more feathers in smelt-eating grebes was again apparent (Fig. 3 right), though only statistically significantly so for the period January–February.

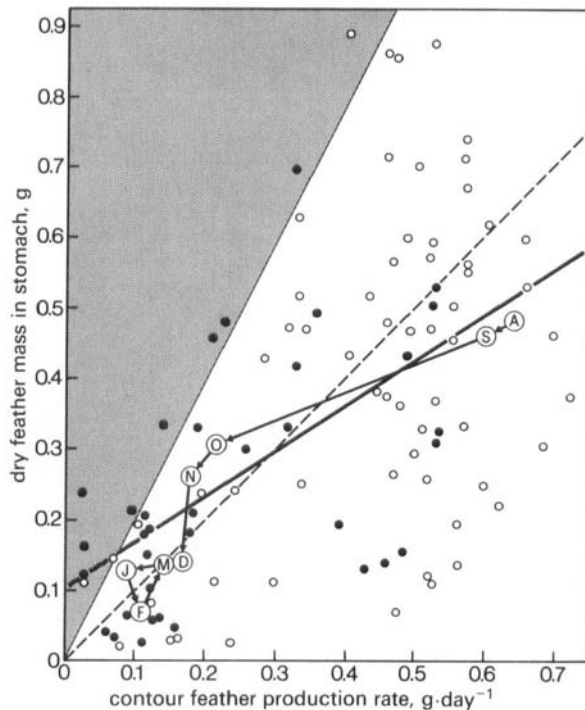


Figure 2. The relationship between the dry feather mass in the stomachs of Great Crested Grebes and the daily contour feather production rate (see text) for adults (O) and juveniles (●). The solid straight line is the best linear fit through all data points, described by  $y = 0.650x + 0.100$ , ( $r^2 = 0.33$ ,  $P < 0.0001$ ). The large open dots are monthly averages for feather mass (from Table 2) plotted against monthly average feather production rates (Piersma unpubl). If the stomachs are emptied every other day by the grebes when they produce a pellet, and if all ingested feathers are their own, then the maximum mass of all stomach feathers should not be more than twice the daily contour feather production rate: only 11 of the 102 data points lie outside the predicted range (■). The dotted diagonal line indicates where daily feather production equals stomach feather mass.

An alternative approach is to use the whole sample and multivariate statistics to find out whether the ingested masses of different fish species can explain some of the variation in stomach feather mass, holding the effect of body moult intensity constant. With the data for 299 grebes, selected to contain the undigested remains of at least 5 g of fish, a multiple regression model was applied to estimate the stomach feather mass (which was logarithmically transformed to achieve normality). Daily contour feather production rate (estimated from dates for grebes for which moult-details were not recorded) was entered first, and the estimated masses of different fish species (also log-transformed) entered second in a stepwise fashion. Daily contour feather production rate had a regression coefficient of +2.61. The estimated ingested masses of perch, pikeperch and smelt explained some of the remaining variation in stomach feather mass, with regression coefficients of, respectively, -0.14, -0.12 and +0.10 (the total explained variance,  $r^2 = 0.26$ ). This suggests that body moult and eating smelt positively affect the presence of feathers in the stomach, whereas eating perch and pikeperch leads to a reduced amount of ingested feathers.

The crucial difference between smelt and the other prey species is that smelt is digested completely, leaving almost no remains other than two small otoliths,

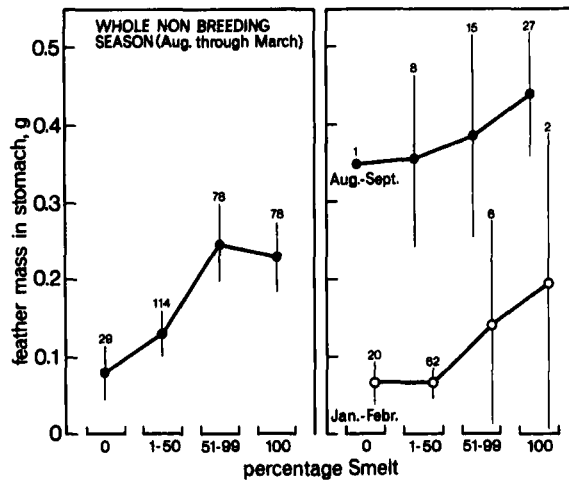


Figure 3. The relationship between the amount of feathers ingested by Great Crested Grebes and the percentage of smelt in their stomachs. Left panel: mean values with 95% confidence intervals from the entire season (one-way ANOVA,  $F = 11.217$ ,  $P < 0.0001$ ). Right panel: the patterns for autumn (●) and midwinter (○) periods with, respectively, a high and a low feather production rate and hence feather intake. For August–September a one-way ANOVA showed no greater variation in ingested feather mass between than within the smelt-percentage categories ( $F = 0.493$ ,  $P = 0.69$ ), but the data for January–February did ( $F = 3.594$ ,  $P = 0.017$ ). Only grebes with the remains of an estimated 5 g or more fish were included.

whereas pikeperch and perch leave many remains other than otoliths in the stomach after digestion (sharp jaws and skull remains, pharyngeal bones, scales and vertebrae). The accompaniment of indigestible fish-remains by relatively few feathers may be explained by the theory that when eating percid or cyprinid fish, grebes eat fewer feathers. Alternatively, eating fish like smelt, which leave very little indigestible matter, might lead to a reduced pellet production rate because the stomach fills more slowly. However, the second explanation is not borne out; the accumulated remains of smelt did not reflect a greater ingested fish mass than the remains of other species. For this reason we believe that when grebes feed on fish species which leave much debris, they eat relatively few of their own feathers.

### Moult, feather ingestion and pellet production in a captive grebe

From 28 August to 9 September 1986 a juvenile female Great Crested Grebe which was found entangled in a net, was kept indoors. The bird was fed with smelt, bream, ruffe and perch from Lake IJsselmeer. Moulded and uneaten feathers as well as ejected pellets were collected each day. When the bird died after 13 days, the contents of stomach and intestines were also analysed. During the first 3 days the grebe produced a small pellet daily. The pellets were much smaller ( $1 \times 2$  cm) than the visual estimate of the size ( $7 \times 5.5$  cm) of a pellet ejected by a free-living adult Great Crested Grebe in New Zealand (O'Donnell 1982). The captive grebe had a strong preference for eating the longest feathers, especially the scapulars (Fig. 4A). If the feathers ejected in the three pellets are compared with the sum of ingested feathers, long feathers appear to be selectively ejected (Fig. 4B), perhaps because long feathers like those of the flanks are particularly suitable for preparing a pellet.



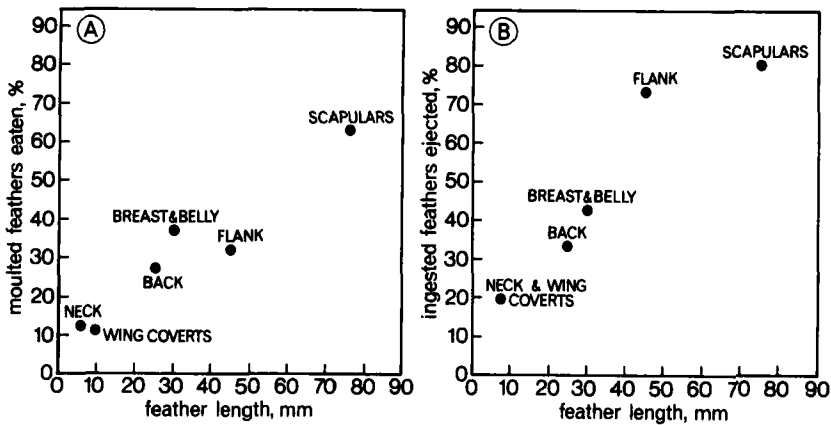


Figure 4. Preferences of a captive Great Crested Grebe for different feather types. In (A) the feathers of each type eaten (sum of pellet and stomach content) are plotted as the percentage of that type which were actually shed during body moult. In (B) the feathers of each type ejected in pellets are plotted as a percentage of the sum of stomach and pellet contents. The total number of feathers examined (moulted and ingested) is about 400.

## Discussion

### Feather eating and feather production

Storer (1961) argued that it was unlikely that a fish-eating species like the Red-necked Grebe *Podiceps grisegena* would be able, in terms of feather production, to form a pellet daily with about 100 feathers. Our data allow this problem to be examined in more detail. If Great Crested Grebes produce one pellet every other day, by which they remove the entire stomach content, the average stomach feather content would represent a day's feather intake, since on average grebes must have been captured halfway between two pellet castings. Indeed, recorded stomach feather masses rarely exceed the estimated 2 days' feather production (Fig. 2). More importantly, average stomach feather masses were always close to, or were less than, the daily contour feather production rate (Fig. 3, Piersma 1988a), i.e. feather ingestion is more than balanced by feather production.

### Functions of feather eating

Several causal and functional explanations have been put forward to account for the unique feather eating habit of grebes. The following four functional hypotheses find most support in the literature:

- (i) feathers are ingested to protect the stomach wall from being damaged by hard and sharp fish-remains (W. Mewes in Madon 1926);
- (ii) digested feathers form a felt-like substance which surrounds the sharp parts of food remains in order to prevent the oesophagus from being damaged when the remains are ejected (Jirsik cited in and supported by Hanzák 1952);
- (iii) ingested feathers form a 'pyloric plug' acting as a filter to prevent sharp and possibly damaging material from entering the intestines (Wetmore 1924, Storer 1969), or to prevent even smaller particles like parasites or their eggs from entering the intestinal tract (Madon 1931);
- (iv) ingested feathers contribute substance to the stomach content enabling the formation of pellets which can be ejected (Madon 1926, Simmons 1956, 1973).

We follow Hanzák (1952) in refuting hypothesis 1, since (a) fish remains were often found in contact with the stomach wall, the feathers being apparently unable to prevent this, and (b) the amount of ingested fish leaving hard and sharp remains was negatively correlated with the amount of ingested feathers in a sample of 299 Great Grebes. The latter argument also leads us to reject hypothesis 2.

A detailed analysis of the intestinal tracts of five Great Crested Grebes and inspection of a lot of faeces showed that no hard parts enter the intestines. Geiger (1957) and Storer (1969) came to the same conclusion. This may be due to the 'pyloric feather plug' acting as an efficient barrier, and this supports hypothesis 3. The inverse relation between the amount of fish debris and the number of feathers does suggest that feathers and fish-remains are complementary. Both may be necessary components to enable the formation of pellets. This supports hypothesis 4. But why is it important to empty the stomach regularly and produce a pellet in the first place?

### **Pellet formation and parasite emission**

Out of the 1540 examined oesophagi and stomachs of Great Crested Grebes none was obviously infested by endoparasitic helminths (nematodes and trematodes). We examined the digestive tracts of sixteen species of fish-eating waterbirds from Lake IJsselmeer (M. R. van Eerden & T. Piersma unpubl.), and found that the gastric parasite load is negatively associated with the habit of producing pellets. The paucity of endoparasites in the upper part of the alimentary tract of grebes compared to species not producing pellets but with an overlapping diet, suggests that regularly emptying the stomach may not only remove the hard remains of fish but also the various stages of ingested helminths or other prospective endoparasites. Producing pellets cleans up stomach and oesophagus. The observations of Storer (1961) on *Podiceps auritus* and *Podilymbus podiceps*, Fjeldså (1981b) on *Podiceps taczanowskii* and J. J. Vlug (pers. comm.) on *P. cristatus* suggest that grebes often drink before ejecting a pellet. It is possible that the alimentary tract can only be properly 'cleaned' if a suitable substrate for pellet formation, either fish debris or ingested feathers, is available, and the compacted remains can be coughed up with the help of a little water.

Even in grebes the proposed cleaning mechanism is not always effective. Lawrence (1950) found nematodes in the stomachs of Western Grebes *Aechmophorus occidentalis*, none of which appeared to be attached to the stomach wall. Fjeldså (1981a) reported that some Taczanowski's Grebes of Lake Junín in Peru contained many stomach parasites, in contrast to the co-occurring grebe species, and suggested that the large parasite numbers might be related to their poor condition. Later on the same lake during a drought (1984–87), local White-tufted Grebes *Rollandia rolland* were in poor condition and full of stomach nematodes (J. Fjeldså pers. comm.).

### **Feather selection**

It is probably no accident that flank feathers are the preferred feather type for ingestion, and predominant among feathers in ejected pellets. Flank feathers are the longest soft feathers and they show a regular curvature (see Fig. 1): features which may help them to wrap up a lot of material efficiently. Another characteristic of the flank feathers that may adapt them for pellet formation is the dark tip, since dark pigments make feather parts more resistant to abrasion (J. Dyck pers. comm.). Indeed, it is likely that the grebes' unique moult of flank feathers, which continues overwinter (Storer & Nuechterlein 1985, Piersma 1988a), can be understood as an

adaptation for providing grebes with a continuous supply of feathers, which enables them to produce pellets regularly and so clean the oesophagus and stomach.

We are grateful to the many people who were involved in the grebe work at various stages. The help of Han Vlug in finding and securing the relevant literature was invaluable. Dick Visser prepared the figures, Ruurd Noordhuis drew a flank feather. The paper was improved by the detailed criticisms of J. FjeldsÅ, K. E. L. Simmons, C. Swennen, J. J. Vlug, referees and the editor.

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