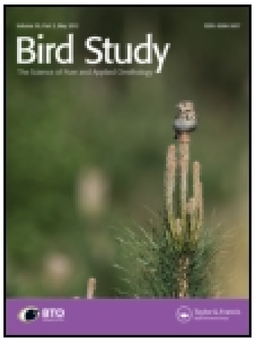

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Body size, nutrient reserves and diet of Red-necked and Slavonian Grebes *Podiceps grisegena* and *P. auritus* on Lake IJsselmeer, The Netherlands

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Samples of Red-necked and Slavonian Grebes that had drowned in gill nets while foraging in winter were analysed for body size, nutrient reserve levels and food content. Measurements of Slavonian Grebes indicated that they may originate from the Icelandic and Norwegian breeding grounds, not from the Baltic area as is suggested in the literature. The mass of the bird after its nutrient reserves have been totally depleted, its 'structural size', is best predicted by different body measurements in each of the 2 species and in the Great Crested Grebe, even though they are closely related. Total fat mass was best estimated from fresh abdominal fat mass in both species. An average Red-necked Grebe in midwinter is estimated to have enough nutrient reserves to survive 11 days starvation. The diet of both species consisted exclusively of fish, mainly Smelt, followed by Perch and Ruffe. Both species took more, smaller Smelt than expected from the food supply that is present in the habitat. This suggests that swimming speeds of the fish may be important in determining whether grebes can catch them, so that food selection may be determined more by the agility of the bird than by its bill dimensions.

This paper documents body size, levels of nutrient reserves and diet of Red-necked Grebes *Podiceps grisegena* and Slavonian Grebes *P. auritus* accidentally collected in gill nets in Lake IJsselmeer, The Netherlands, during the non-breeding season.

Red-necked Grebes breed over much of eastern and north-eastern Europe.[1,2] In winter, Red-necked Grebes from the European breeding areas are widely distributed over the coastal areas of Europe, with important wintering concentrations in the Danish straits,[3] and along the west coast of Norway.[4] Slavonian Grebes from breeding areas in Sweden, Finland and the western Soviet Union are also thought to winter in coastal areas southward to Brittany.[5] In winter, both species occur regularly but always in small numbers (less than 100) in The Netherlands.[6,7] They are mainly found on the open waters of the North and Wadden Seas and the Delta area (all marine) and in Lake IJsselmeer (freshwater). Lake IJsselmeer provides abundant potential prey (for example Smelt *Osmerus eperlanus*[8]), so the small number of grebes there is somewhat puzzling. Study of their body composition and stomach contents might indicate a possible food shortage.

A nutrient reserve can be defined as the quantity of metabolizable nutrients (fat and protein) above a residual level. The total mass of the body is made up of the nutrient reserves plus the 'structural size', which is largely determined by the skeletal dimensions of the bird.[9] Structural size can be estimated from the mass of birds that have depleted their nutrient reserves, that is, starved birds.[10] Individuals differ in structural size: I have tried to find out which body dimensions best predict operational structural size, the mass of starved birds.

The presence of body fat and protein reserves allows birds to overcome periods of food shortage and, if necessary, to spend time in places other than those in which they feed. The material on which this paper is based has allowed me to estimate levels of nutrient reserves in Red-necked and Slavonian Grebes and to develop equations that allow reserve levels to be estimated from body measurements.

Because they feed underwater it is generally impossible to study the diet of grebes by direct observation: stomach contents must be studied instead. The diet of Red-necked[11,12,13] and Slavonian Grebes[12,14] has been studied at several breeding locations but the only studies in the winter quarters are of Red-necked Grebes in Denmark.[3,15] Fjeldså[3] found that Red-necked Grebes with relatively long, slender bills fed mostly on pelagic prey (squid and fish) and that those with shorter and thicker bills fed mainly on benthic invertebrates (polychaetes). On a wider geographical scale, Fjeldså[3,16,17] has documented a number of situations where bill morphology and choice of prey are correlated, both within and between grebe species. It is therefore of interest to see whether this is also true for the relatively large-billed Red-necked and small-billed Slavonian Grebes collected at comparable feeding localities in Lake IJsselmeer.

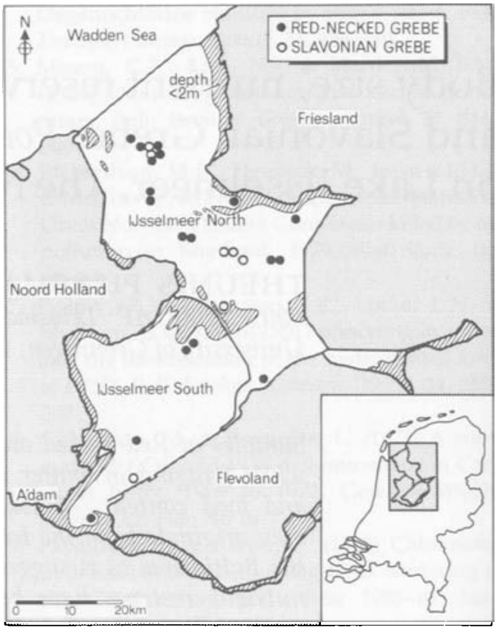

Figure 1. Lake IJsselmeer, showing places where Red-necked and Slavonian Grebes were captured in gill nets. The capture location of one juvenile female Red-necked Grebe is unknown.

STUDY AREA AND METHODS

Lake IJsselmeer (Fig. 1) was created in 1932 by the closure of the large dyke that connects Friesland and Noord-Holland. Since then, several large land-reclamation schemes have been carried out, reducing the open water surface by 45% to 1850 km^2. In 1975 another dyke was closed, splitting Lake IJsselmeer into 2 parts (IJsselmeer North, 1150 km^2 and IJsselmeer South, 700 km^2). Apart from some trenches as deep as 15 m, IJsselmeer North is 4–6 m deep with a rather flat sandy bottom; there is soft clay only in the deep trenches. IJsselmeer South is 3.5–4.5 m deep, with a uniform flat bottom of soft silt and clay. Lake IJsselmeer is a eutrophic freshwater basin fed mainly by the polluted river Rhine. It has large fish stocks (300–500 kg ha^{-1}),[8] heavily exploited by people.

Grebes were collected fresh from fishermen around Lake IJsselmeer during the winters of 1979–1985 (September–March). Twelve of the 19 Red-necked Grebes and 6 of the 7 Slavonian Grebes were found in late 1980, although sampling intensities were comparable throughout the 7 winters. All the grebes had drowned accidentally in commercial gill nets standing 1.2 m high on the lake bottom. The depths (m) of the bottom at the points of capture were:

	Mean	*SD*	*Range*	*Sample size*
Red-necked	5.2	2.1	2.0–12.5	18
Slavonian	3.7	1.2	1.5– 4.5	7

The difference in mean depth is not statistically significant ($t = 2.1$, $0.1 > P > 0.05$). Only small numbers of Great Crested Grebes *P. cristatus*, and the flock-feeding Goosanders *Mergus merganser* and Red-breasted Mergansers *M. serrator* were caught at the same time as the Red-necked and Slavonian Grebes, indicating that these 2 species foraged relatively solitarily. Most Red-necked and Slavonian Grebes were captured centrally in IJsselmeer North (Fig. 1). In addition to these drowned but healthy grebes, 6 starved Red-necked Grebes, collected along the North Sea coast of Noord-Holland, were examined.

The birds were stored in freezers (at −15° to −20°C) immediately after collection. After thawing they were weighed and measured. To correct the fresh body mass for variable amounts of water in the plumage, I multiplied by 0.978 in 'moist' birds, 0.931 in 'wet' ones, and 0.913 in 'very wet' ones, these values being derived from experiments. I furthermore subtracted the fresh mass of fish in the oesophagus and also the average fresh mass of the stomach content (which is on average 12 g in Red-necked Grebes and 8 g in Slavonian Grebes). The measurements taken were: body length (length of the stretched bird from bill tip to end of body (grebes have only a tiny tail), cm); exposed culmen length (mm); tarsus length (length of the metatarsus, from the posterior side of the ankle joint to the distal end of the metatarsus, with the foot flexed at right angles to the tarsus, mm); wing length (straightened chord, mm); keel length (length of the ventral ridge of the keel of the sternum, measured after dissection, mm). In a sample of 38 Red-necked Grebes from The Netherlands, measured at the Zoological Museum in Amsterdam, culmen length was positively correlated with both bill height ($r = 0.30$, $P = 0.035$) and bill width ($r = 0.38$, $P = 0.009$). Culmen length is therefore a measure of overall bill size.

The grebes were sexed by gonadal examination and aged as first-year or adult by the presence or absence, respectively, of brown lesser upper wing coverts (to be published) and by bill colour,[1] with a check on the gonads in females. The abdomen was opened and the abdominal fat deposit, which is an easily separable layer of fat, ventral and lateral to the intestines, removed by taking it from the intestines and cutting it near the cloaca.

After dissection the carcases, including the abdominal fat, were dried to constant mass at 70°C and weighed again. The dried carcases were then fragmented and the fat extracted in Soxhlet-extractors for 40–50 hr, using petroleum-ether (boiling between 40 and 60°C). The fat-free remains were dried again for 2–3 hr at 70°C and weighed. Total fat mass was obtained by subtracting the fat-free dry mass from total dry mass.

Food was studied from oesophageal and stomach contents. Fish in the oesophagus were never digested and their total length could be measured directly. Stomach contents, comprising a ball of body feathers with fish debris, were stored in 96% ethanol. All stomachs contained at least 10 feathers, which were floated off from the heavier fish fragments by water flow in a 2 l measuring glass, the overflow being checked for food remains. The fish fragments consisted of vertebrae, scales, otoliths, parts of jaws and pharyngeal bones. The lengths of the right otoliths of Smelt, Ruffe *Gymnocephalus cernua* and Perch *Perca fluviatilis*, and of the right pharyngeal bones of Bream *Abramis brama* and Roach *R. rutilus*, were measured to the nearest 0.1 mm with a micrometer mounted on a binocular microscope. The total number of right side fragments was taken as the total number of fish in the stomach. Total fish length and fresh mass are, respectively, linearly and exponentially related to otolith or pharyngeal bone-lengths. The predictive equations are listed in Table 1.

The wings of 6 Red-necked Grebes were deposited in the collection of the Zoological Museum in Amsterdam under reference numbers ZMA 37008, ZMA 37012–16. Flat skins of 3 other Red-necked Grebes were deposited under reference numbers ZMA 37009–11. The right wings of the 7 Slavonian Grebes were stored under numbers ZMA 37001–7.

Most statistical analyses used the standard SPSS package. Non-parametric statistical tests were performed according to Siegel.[18]

RESULTS

Body size

Table 2 summarizes the body dimensions of the Red-necked and Slavonian Grebes from Lake IJsselmeer. For all measurements, males were slightly, but non-significantly, larger than females. The measurements of Red-necked Grebes are close to those given by Cramp & Simmons.[1]

In Slavonian Grebes there is sufficient geographical variation in body size of European breeding birds to evaluate the origin of the

Table 1. Equations to estimate total fish length (cm) and fresh mass (g) from otolith (OL) or pharyngeal bone (PL) lengths (mm) or total fish lengths (FL, cm) in a series of fish species fed upon by grebes in Lake IJsselmeer (after Piersma & Muller[33]). The coefficient of determination (r^2) is the proportion of variance explained by the relationship with the independent variable (OL, PL or FL).

Species	*Y = length or mass*	*Equation*	r^2	*n*
Smelt	Length	$Y = 3.41\ OL - 0.479$	0.97	17
	Mass	$Y = 0.1202\ OL^{3.252}$	0.97	17
	Mass	$Y = 0.0028\ FL^{3.231}$	0.99	17
Bream and Roach (combined)	Length	$Y = 1.49\ PL + 1.472$	0.99	27
	Mass	$Y = 0.0629\ PL^{2.920}$	0.99	27
	Mass	$Y = 0.0030\ FL^{3.501}$	0.99	27
Ruffe	Length	$Y = 2.14\ OL - 0.362$	0.98	13
	Mass	$Y = 0.0554\ OL^{3.447}$	0.98	13
	Mass	$Y = 0.0075\ FL^{3.228}$	0.99	13
Perch	Length	$Y = 2.81\ OL - 0.340$	0.67	13
	Mass	$Y = 0.1140\ OL^{3.526}$	0.75	13
	Mass	$Y = 0.0086\ FL^{3.073}$	0.99	13

Slavonian Grebes wintering in The Netherlands. The measurements (Table 2) generally agree better with those presented by Fjeldså of Icelandic and Norwegian specimens than with the smaller Baltic specimens[5] (Fjeldså's presentation of the data does not allow statistical testing of the differences). This may indicate a more northern and northwestern breeding origin (Norway, Scotland, Iceland) than has been supposed.[1,5]

One of the 2 Red-necked Grebes collected in September, a female (ZMA 37008), was in (simultaneous) wing moult. Measurements of the growing primaries, with reference to full-grown primaries in another adult female (ZMA 37009), showed that the primaries were about 85% grown.

Body composition

The 6 starved Red-necked Grebes had a mean mass of 494.4 g and a mean content of 2.5 g of extractable fat. This is only 1.5% of the level of fat in healthy Red-necked Grebes in winter (see below), which implies that almost the entire fat store is depleted during starvation. Thus the total fat content of an individual is a good measure of its fat reserve. Table 3 shows that fat-free body mass is correlated with all measured body dimensions, with tarsus

Table 2. Body dimensions of freshly drowned Red-necked and Slavonian Grebes from Lake IJsselmeer. The figures are means, with standard deviations and sample sizes in parentheses. There was only one female Slavonian Grebe, an adult. Differences between adult and juvenile birds and between males and females were not statistically significant (Student's t-tests, $P > 0.05$). All lengths in mm, mass in g

	Red-necked Grebes				*Slavonian Grebes*		
Dimension	*Males*		*Females*		*Males*		*Females*
Body length	443	(19 ,10)	415	(14 ,8)	340	(10 ,5)	300
Wing length	178.5	(8.0,11)	170.3	(4.0,7)	145.8	(3.2,6)	132
Culmen length	44.1	(3.1,10)	37.8	(1.9,8)	25.0	(2.2,6)	21
Tarsus length	55.5	(3.4, 9)	51.7	(2.4,6)	44.8	(2.5,6)	42
Keel length	67.6	(6.1,11)	62.6	(4.2,8)	60.4	(1.5,5)	56
Body mass	873.5	(124 ,11)	785.4	(97 ,8)	502.3	(54 ,6)	393

Table 3. Relationships between fat-free body mass and various body measurements (plus 2 combinations of 3 measurements) in starved Red-necked Grebes (4 males, 2 females). All the (length) measurements were in mm. Mean fat-free mass was 491.9 g. The regression equation allows the fat-free body mass to be predicted from body measurements

Independent variable (X)	*Mean value*	r^2	*Regression equation (Y = fat-free body mass)*
Body (B)	405.0	0.66	$Y = 3.18\ X\ 797.6$
Wing (*W*)	180.7	0.55	$Y = 7.21\ X - 811.4$
Culmen (*C*)	41.5	0.76	$Y = 21.19\ X - 387.5$
Tarsus (*T*)	53.5	0.82	$Y = 12.63\ X - 183.6$
Keel (*K*)	67.5	0.74	$Y = 13.43\ X - 414.4$
$C \times T \times K \times 10^{-3}$	152.2	0.92	$Y = 2.19\ X + 158.2$
$B \times W \times C \times 10^{-4}$	305.7	0.79	$Y = 1.45\ X + 49.0$

length being the best single predictor of fat-free mass. (I have not taken fat-free *dry* mass since water content was very much the same in all grebes, both starved and healthy ones. It varied between 63 and 65%.) Since the mass of a bird depends essentially on its volume, I have looked for the best three-dimensional combination of body measurements to estimate structural size, as done earlier for Great Crested Grebes.[10] This is the product of culmen, tarsus and keel length (Table 3), which is actually the best of all possible multiplication of 2 or 3 body dimensions.

Keel length cannot be measured on live birds, and tarsus length only with difficulty under field conditions. The combination of 3 more easily measured dimensions which best predicts structural size is the product of body,

Table 4. Relationships between total fat mass and body mass, abdominal fat mass and several combinations of body mass and structural size variables, in healthy Red-necked and Slavonian Grebes from Lake IJsselmeer. The structural size variables Body length (*B*), Culmen length (*C*) Tarsus length (*T*), Wing length (*W*), and Keel length (*K*) were added to the predictive equations of fat from body mass with stepwise multiple regression techniques. Stars indicate the predictive equations advised for use elsewhere. Note that body mass refers to the mass of the 'dried and emptied' birds. In practice this means subtracting 12 and 8 g, respectively, from the fresh mass of Red-necked and Slavonian Grebes with a dry plumage, and weighed 1–2 hr after capture. All lengths in mm, masses in g

Independent variable(s) (X)	r^2	*Regression equation (Y = total fat mass)*	
Red-necked Grebes (n = 14)			
Body mass*	0.35	$Y = 0.37\ X$	−157.9
Abdominal fat mass*	0.86	$Y = 14.60\ X$	+ 53.1
Body mass(1), Culmen(2)	0.44	$Y = 0.44\ X_1 - 5.18\ X_2$	− 1.5
Body mass(1), Tarsus(2)	0.49	$Y = 0.51\ X_1 - 8.70\ X_2$	+189.3
Body mass(1), $(C \times T \times K \times 10^{-3})$(2)*	0.60	$Y = 0.62\ X_1 - 1.33\ X_2$	−167.0
Body mass(1), $(B \times W \times C \times 10^{-4})$(2)*	0.67	$Y = 0.57\ X_2 - 0.75$	− 88.7
Slavonian Grebes (n = 6)			
Body mass*	0.74	$Y = 0.27\ X$	− 34.0
Abdominal fat mass*	0.87	$Y = 8.94\ X$	+ 41.4
Body mass(1), Culmen(2)	0.74	$Y = 0.26\ X_1 + 0.53\ X_2$	− 42.6
Body mass(1), Tarsus(2)*	0.90	$Y = 0.40\ X_1 - 4.62\ X_2$	+110.5
Body mass(1), $(C \times T \times K \times 10^{-3})$(2)	0.76	$Y = 0.31\ X_2 - 0.36\ X_2$	− 26.9
Body mass(1), $(B \times W \times C \times 10^{-4})$(2)	0.74	$Y = 0.29\ X_1 - 0.09\ X_2$	− 32.1

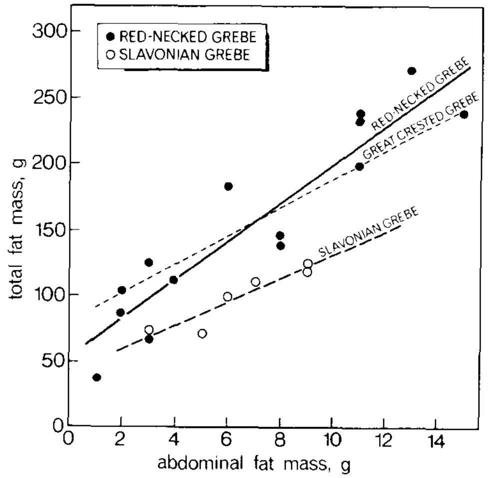

Figure 2. Relationship between fresh abdominal fat mass and total body fat in Red-necked, Slavonian, and Great Crested Grebes. The regression equations are: Red-necked $Y = 14.6 \quad X+53.1 \quad (r^2 = 0.86,$ $n = 14)$, Slavonian $Y = 8.9 \quad X+41.4 \quad (r^2 = 0.87,$ $n = 6)$, Great Crested $Y = 10.6 \quad X+81.2 \quad (r^2 = 0.85,$ $n = 42)$[10].

wing and culmen length, which is the only improved estimator of structural size over one-dimensional estimators.

Table 4 shows that, in both Red-necked and Slavonian Grebes, total fat mass is positively correlated with body mass. However, in both species abdominal fat mass is a much better predictor of total fat mass than is body mass (Table 4 and Fig. 2). Abdominal fat mass is also a good predictor of total fat mass in Great Crested Grebes and in many other bird species.[10,19–23]

Unfortunately, abdominal fat mass is only measurable in dead birds, so we are in need of a better predictor of total fat mass for live birds than body mass. The latter is a relatively poor predictor since it reflects variation not only in nutrient reserve levels but also in structural size. For this reason, I have included various body dimensions with body mass as predictors of total fat mass (Table 4). In Red-necked Grebes, inclusion of culmen or tarsus length in the regression gives improvements of 9 and 14% explained variance over the regresssions with body mass only. Inclusion of the three-dimensional predictors of fat-free body mass gives an improvement of 25–32% (Table 4). In Slavonian Grebes, body mass alone is a good predictor of total fat mass but the inclusion of tarsus length in a multiple regression model still gives an increase in explained variance of 16%. Inclusion of other parameters gave no improvement. This may imply that structural size of Slavonian Grebes is determined differently from that of Red-necked Grebes.

The equations recommended to predict fat content in Red-necked Grebes and Slavonian Grebes for use in studies elsewhere are indicated in Table 4. Because of the small sample sizes available, it was not possible to test the predictive equations on independent samples, a procedure recommended by some authors.[24,25]

With equations to estimate structural size (for Red-necked Grebes only) and fat content from length measurements and body mass, it is possible to estimate the total nutrient

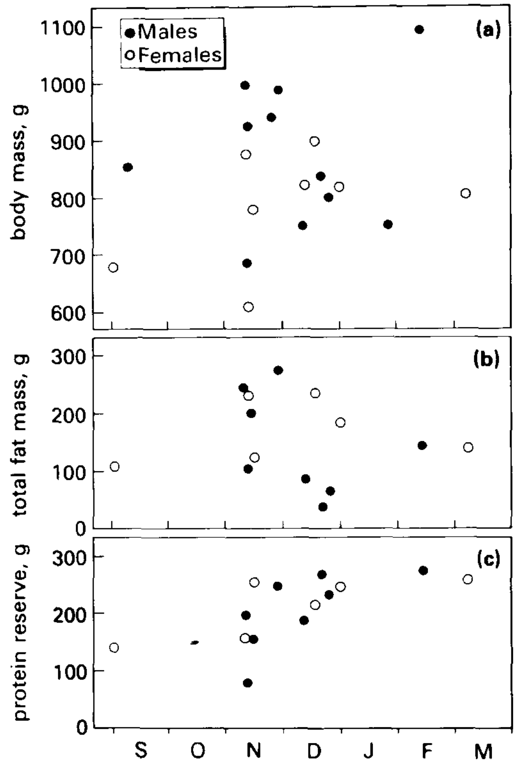

Figure 3. Seasonal variations in body mass and in fat and protein reserve levels of Red-necked Grebes from Lake IJsselmeer. See Table 5 and text for methodology. Data from all birds are included in (a) but only data from individuals for which total fat mass was actually determined are included in (b) and (c).

reserve. Body mass minus estimated total fat mass gives estimated fat-free mass. Estimated fat-free mass minus estimated structural size gives estimated protein reserve mass. Total fat mass plus protein reserve mass gives the total nutrient reserve level.

Figure 3 shows how body mass, total fat mass and protein mass of individual Red-necked Grebes varied over the winter. Body mass and total fat mass did not change systematically. (The wing-moulting female from early September had a fat content comparable to the winter birds.) Lowest values of protein reserve mass were found in September and November, and were somewhat higher later. Since levels of nutrient reserves changed little over the winter, I have calculated mean values for the whole season for both species (Table 5). None of the differences between the 2 species or between the 2 sexes of Red-necked Grebes is statistically significant.

The total nutrient reserve level of Red-necked Grebes averages 363 g or 43% of body mass (Table 5). Dry fat has an energy content of 38.0 kJ/g and dry muscle (protein content 90%) yields 16.4 kJ/g.[26] Assuming that the protein reserve contains 70% water and 30% dry muscle, the energy content of the total nutrient reserve mass amounts to $(207.7\times0.3\times16.4 = 1022 \text{ (protein)})+(155.3\times38.0 = 5901 \text{ (fat)}) = 6923$ kJ. With an average body mass of 852 g, Kendeigh's[27] formula for the existence energy of a non-passerine bird (starving birds are generally inactive), at an air temperature of 0°C ($\log \text{EE (kCal/day)} = 0.6372+0.53 \log \text{BM (g)}$) gives an estimated daily energy need for a starving Red-necked Grebe in winter of 648 kJ. This implies that a healthy Red-necked Grebe with average winter reserve levels could survive about 6923/648 = 11 days without food.

Food

The diet of Red-necked and Slavonian Grebes from Lake IJsselmeer in terms of prey numbers and prey mass in the guts is summarized in Table 6. Both species fed exclusively on fish, except that a Red-necked Grebe contained a jaw of a polychaete worm (probably Nereidae, which do not occur in Lake IJsselmeer). Smelt was the most important prey for both grebes and was almost the only prey species of the Slavonian Grebes, though the diet of the Red-necked Grebes was a little more varied.

The length distributions of the Smelt, Ruffe and Perch found in Red-necked and Slavonian Grebes are presented in Fig. 4. Fish lengths varied between 2 and 12 cm. Although the bill of Red-necked Grebes is almost twice as large as the bill of Slavonian Grebes, the average length of Smelt taken by the latter species is larger than the average length of Smelt eaten by Red-necked Grebes. The few Perch taken

Table 5. Average nutrient reserves of Red-necked Grebes and Slavonian Grebes from Lake IJsselmeer. Only data from fully analysed birds are incorporated. Protein reserve mass was obtained by subtracting structural size from fat-free body mass. Structural size was estimated from the multiplication of culmen, tarsus and keel (see Table 3). The fat index is (total fat mass/body mass)×100%. The protein reserve index is (protein reserve mass/body mass-total fat mass))×100%. All masses in g

	Red-necked Grebes				*Slavonian Grebes*	
Nutrient reserve variable	*Males (n = 8)* *Mean*	*SD*	*Females (n = 6)* *Mean*	*SD*	*(n = 6)* *Mean*	*SD*
Body mass	884.0	136.7	809.4	77.2	488.3	70.5
Total fat mass	143.5	85.4	171.1	55.0	99.5	22.5
Fat index	15.7%	8.0%	20.8%	5.0%	20.2%	2.6%
Protein reserve mass	204.1	65.3	212.4	52.3	—	—
Protein reserve index	27.1%	6.9%	33.1%	7.1%	—	—

Table 6. Diet of Red-necked and Slavonian Grebes from Lake IJsselmeer as determined from oesophagus and stomach contents. 18 Red-necked and 6 Slavonian Grebes were examined. See text for methodology and see also Table 7

	Red-necked Grebes		*Slavonian Grebes*	
Fish species	*Percentage by number*	*Percentage by mass*	*Percentage by number*	*Percentage by mass*
Smelt	88.8	61.3	95.6	94.2
Bream	0.6	8.0	0	0
Roach	0.3	0.4	0	0
Ruffe	4.1	12.3	0	0
Perch	6.2	18.0	4.4	5.8
Total number and total mass	338	518 g	135	205g

by Slavonian Grebes tend to be smaller than the majority of Perch in Red-necked Grebes (Fig. 4).

There was no correlation between culmen length of an individual and the average length of the Smelts taken by that individual in either species. (Correlation coefficients are 0.33 for Red-necked and −0.05 for Slavonian Grebes, neither being statistically significantly different from zero.)

The majority of the identified prey were found in the stomach (Table 7). Only 3 out of 18 Red-necked Grebes and 2 out of 6 Slavonian Grebes had freshly ingested fish in their oesophagus. The average total fish mass corresponding to the remains in the gut, differed little between the 2 species, despite the large difference in body mass.

DISCUSSION

Structural size of closely related species

In Great Crested Grebes body length, wing length and keel length are the best three estimators of structural size (fat-free mass of starved birds[10]). For the closely related Red-necked Grebe, keel, tarsus and culmen length were the best 3 estimators and in Slavonian Grebes only the inclusion of tarsus length improved the predictive equation of total fat mass from body mass alone, implying that in this species structural size is determined by yet other dimensions. This finding should make us realize that structural size cannot be estimated from a general set of body measurements, but has to be determined for

Table 7. Average fish contents of freshly drowned Red-necked and Slavonian Grebes from Lake IJsselmeer. Content of oesophagus is based on counts of intact, undigested fish. Stomach content was estimated from numbers and size of right-side otolith or pharyngeal bones (see text for details)

	Red-necked Grebes (n = 18)			*Slavonian Grebes* (n = 6)		
Category	*Mean*	*SD*	*range*	*Mean*	*SD*	*range*
Number of Smelts in oesophagus	0.4	1.8	0– 7	0.3	0.8	0–2
Number of Smelts in stomach	16.4	19.6	0–63	21.3	16.9	2–45
Number of other fish in oesophagus	0.7	2.9	0–12	0.2	0.4	0–1
Number of other fish in stomach	1.3	2.5	0–10	0.7	1.2	1–3
Total number of fish remains	18.9	20.5	0–64	22.5	16.5	2–46
Total fish mass(g)	28.8	29.1	0–82.1	34.2	21.8	1–66.5

each species separately, even if they are closely related.

Food intake

The equation of Nilsson & Nilsson[28] to estimate daily food consumption from fresh body mass in fish-eating birds predicts that an 840-g Red-necked Grebe and a 500-g Slavonian Grebe require, respectively, 156 g and 100 g fresh fish per day. In experiments with captive adult Red-necked Grebes, fed with a mixed diet of water-insects and fish,

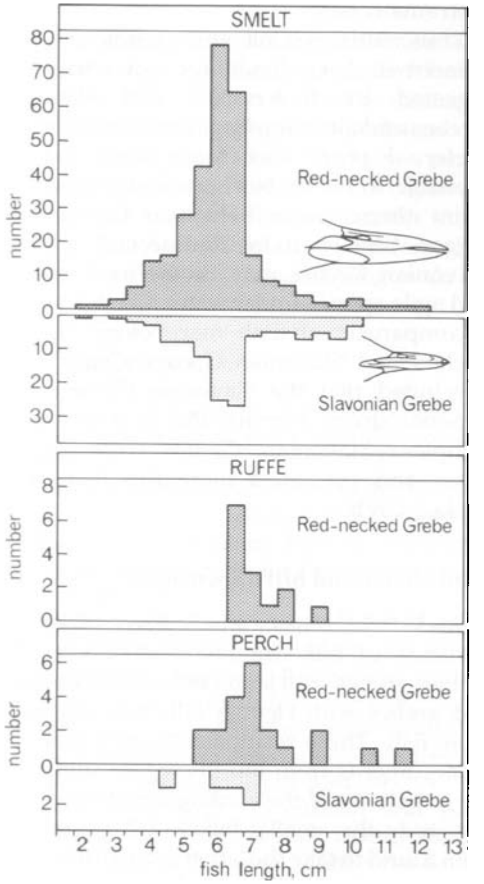

Figure 4. Frequency distributions of total length of Smelt, Ruffe and Perch found in oesophagus and stomach contents of freshly drowned Red-necked and Slavonian Grebes from Lake IJsselmeer. The length of fish in stomachs was estimated from otolith length (see Table 1). The dimensions of the bill are to scale with the x-axis. The average length of Smelt taken by Slavonian Grebes (mean = 6.53 cm, SD = 1.61 cm, n = 129) is larger than that of Smelts taken by Red-necked Grebes (mean = 5.99 cm, SD = 1.32 cm, n = 300; t = 3.35, $p < 0.001$, Student's t-test). The two Bream and one Roach in Red-necked Grebes are not shown, but measured 11.5, 11.4 and 5.2 cm, respectively.

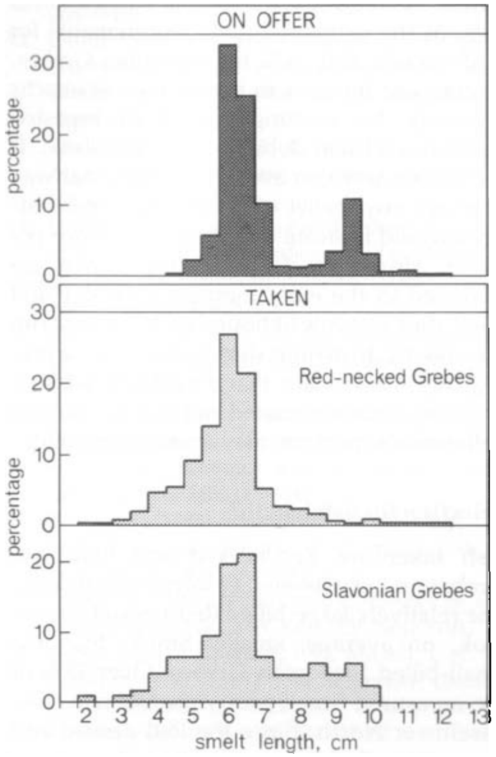

Figure 5. Frequency distribution of lengths of Smelt present in the northern part of Lake IJsselmeer in autumn (top graph, sample size about 1900) compared with the length distributions of Smelts taken by Red-necked and Slavonian Grebes (bottom, from Fig. 4). We sampled the fish populations of the northern part of Lake IJsselmeer with a 7-m wide, small-meshed beam-trawl on 10 October 1985 (see Piersma & Muller[33] for details). There is little difference in the growth and date-specific size of Smelt between years (R. Lindeboom, pers, comm.). The average 'capture-date' of Smelts found in the grebes is 14 December. Since the growth rate of Smelts in late autumn is small, the length distribution of Smelts in early October should be close to the length distribution of Smelts in December. The truncated distribution of the top graph is not a result of 3–5-cm fish not being captured by our equipment: in July 1986 first-year Smelt of 2–5 cm were abundant in the catches (R. Lindeboom, pers. comm.). Both grebes take more of the small Smelt than expected by chance (for Red-necked Grebes: χ^2 = 7010, d.f. = 10, $P < 0.001$; for Slavonian Grebes: χ^2 = 1470, d.f. = 8, $P < 0.001$).

Markuze[13] found a daily intake of 180 g per bird, which is comparable to 156 g of fish as the energetic density of insects is generally lower than that of fish.[29] The average mass of fish whose remains were found in the guts was 22% of the estimated daily requirements for Red-necked and 34% for Slavonian Grebes. Grebes are thought to empty their stomachs regularly by ejecting pellets of ingested feathers and fish debris (to be published). If the grebes were on average captured halfway between two pellet ejections, these percentages would indicate that they do so twice per 24 hr. However, since the fishing nets are removed in the early morning each day and reset after a couple of hours, grebes do not run the risk of drowning during their full 'working' day. This means that the relative intake is probably underestimated and that the derived pellet production rate may be an overestimate.

Selection for fish length?

Fish taken by Red-necked and Slavonian Grebes on Lake IJsselmeer were 2–12 cm long. The relatively large-billed Red-necked Grebes took, on average, smaller Smelts than the small-billed Slavonian Grebes. Over 95% of the measured Smelt prey were taken in Lake IJsselmeer North. Since the Red-necked and Slavonian Grebes were collected at comparable depths in about the same area in IJsselmeer North, the differences in length of consumed Smelt may probably be explained by differences in the mode of foraging. It is therefore of interest to compare the length distribution of Smelts taken by the two species with the length distribution of Smelts present in Lake IJsselmeer (Fig. 5). Two age classes are identifiable (a first-year and a second-year class). Figure 5 shows that the most abundant size classes of Smelt (6.0–6.5 cm) are also the best represented in the stomach contents of the grebes. However, both species, especially Red-necked Grebes, take many more of the small-sized Smelts than expected by chance. Red-necked Grebes take very few second year Smelts. Slavonian Grebes take more, but only the smallest individuals. How may this relative predominance of small Smelts in the diet of Red-necked and Slavonian Grebes be explained?

Sustained and burst swimming speeds of fish are both linearly or even exponentially related to fish length.[30] Additionally, the length of time that fish are able to swim at burst speeds, which is obviously important for fish trying to escape from pursuing predators, is also dependent on fish length: in Herring *Clupea harengus*, endurance is a function of the fourth power of length![31] Large Smelts must therefore be much more difficult to catch than small ones.

Thus, although all size classes of Smelt present in Lake IJsselmeer can actually be ingested by Red-necked and Slavonian Grebes and although large Smelt might be the preferred prey, such large Smelt are not available to the grebes because they can outswim them. Since Slavonian Grebes take bigger Smelts than Red-necked Grebes, Slavonian Grebes may be the more speedy and agile species under water. On the basis of a comparison of limb morphology of Red-necked and Slavonian Grebes, Onno[32] also concluded that the Slavonian Grebe is the superior diver. Perhaps this is why, in my samples, Slavonian Grebes were slightly fatter and contained more fish than Red-necked Grebes.

Food choice and bill dimensions

Fjeldså[3,14,16,17] has emphasized the importance of bill size for food selection in grebes: grebes with larger bills take larger prey and grebes with slender bills take relatively more fish. These relationships are supported by arguments from morphological studies of the adaptivity of the feeding apparatus.[3,16] In my study the smaller-billed of 2 species has been found to take the larger individuals of the main prey species, possibly because it is more agile. However, when we compare total diet instead of Smelt only, the large-billed species certainly took the largest prey. Red-necked Grebes fed on 3 species, Bream, Roach and Ruffe, which were not fed upon by Slavonian Grebes, and all 3 have thicker bodies than Smelt (the ratio of maximum height to maximum length being, respectively, 0.34, 0.29 and 0.25 compared with 0.15). When several species of prey are involved, cross-section rather than length may be the most important parameter to compare with bill size of the predator.

Scarcity on Lake IJsselmeer

Measurements of body condition and of stomach contents indicated that Red-necked and Slavonian Grebes are able to make a living on Lake IJsselmeer in winter. Their scarcity in this area must therefore be due to factors other than local food availability.

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